The Botanical Review

Interpreting Botanical Progress

45066

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Volume XXI
1955

The Botanical Review

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THE BOTANICAL REVIEW

TREE GROWTH

I. Some Historical Chapters

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"Fraget die Bäume! Besser als alle Bücherweisheit werden
sie euch sagen, wie sie behandelt sein wollen".

—Theodor Hartig

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INTRODUCTION

Observations on the manner in which trees carry on the processes of growth must have antedated the historic era; the sequence from seed to germination, to seedling, to sapling, and from young tree to mature tree must have been observed by primitive man in all parts of the world, even before the Stone Age. Also lost in the fogs of prehistory are the first observations on the annual length growth of branches and on the formation of growth "rings" in the wood, although there can be no doubt that these phenomena, too, were observed if not understood in very early times.

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[1] Sincere thanks are given to Mr. R. C. Janeway, Librarian, Texas Technological College, for his understanding help in making available through interlibrary loan many hundreds of books and articles which could not otherwise have been examined, and to the Bibliographical Center for Research at Denver, Colorado, for processing a large part of these loans.

The mists of early written history are almost as impenetrable as are the fogs of prehistory. What was known by the several early civilizations which ranged all the way from China to the Nile and which covered a period of several millenia, is virtually a blank page to us. They do not seem to have left records of any knowledge whatsoever of the growth of plants. And some writings, known once to have existed, have been lost. Thus Aristotle's works are said (Kieser, 1812) to contain some fragmentary references to botanical writings by the Greek author Empedocles of Agrigentum (c. 450 B.C.) who was perhaps the first, at least in the western world, to have written on botanical subjects.

The present historical review is intended less as a complete history of our knowledge of the growth of trees than as a record, in a large measure forgotten today, of the early development of certain fundamental ideas; in other cases, new interpretations are given to some well-known subjects.

THEORY OF BUD-ROOTS

The earliest written observation on the growth of trees which has come to our attention occurs in a Hippocratic collection, discussed in Cohen and Drabkin (1948). The date of this collection is not given but, if not written by Hippocrates himself (c. 450–357 B.C.), it probably lies between his time and that of Aristotle (384–322 B.C.). Quoting: " Now if buds are taken from trees and inserted into other trees, and, becoming trees themselves, live on these other trees and bear fruit, the fruit is unlike that of the trees upon which they have been grafted. This comes about as follows. First the bud sprouts, for it has nourishment originally from the tree from which it was taken and then in that upon which it was grafted. When it has sprouted in this way it sends out tender roots to the tree and at first derives nourishment from the moisture of the tree upon which it has been grafted. Then after a time it sends roots into the ground through the tree upon which it has been grafted and derives nourishment from the soil, drawing up moisture. It is from this source that it is fed. Hence one should not be surprised to find that grafts bear fruit different from that of the trees upon which they are grafted. For they live from the earth ". The term " grafting " is here used in its broader sense to include budding. E. H. F. Meyer (1854, Vol. 1) and

Unger (1855) refer to this theory under writings called Pseudo-Hippocrates, dated 424 B.C. A. Braun (1853) stated that Moquin-Tandon, in his "Teratologie", cited Hippocrates on individuality in plants.

This very early hypothesis, here applied to the artificial process of budding, was soon to be used as an explanation of the natural growth of buds on trees and shrubs, to become extended in its scope and details, and to be claimed as an original theory by several later botanists, even into the nineteenth century. It has been called the "theory of descending vessels" and "the theory of phytons", in addition to "the bud-root theory".

Whether Aristotle himself wrote a treatise on botany is not certain; he is given credit for discussing individuality of buds and branches by Schulz (date?) and by Wimmer (1838). His pupil and successor, Theophrastus of Eresus (c. 372–287 B.C.), wrote voluminously on the science of plants; just how much of his work was original and how much merely a repetition of the knowledge of his master is unknown. Strömberg (1937) states that Theophrastus had access to a rather comprehensive literature on the subject of botany, written before his time. In any event, although Theophrastus himself did some traveling, much of his compilation is based on the verbal reports of men who accompanied the army of conquest of Alexander the Great and of other travelers in the Near East and especially in Egypt. Hence much of his information must have been the common knowledge of the vinyardist, of the olive and date culturist, of the cultivator of fruits and grains, and of the rhizotomist or collector of roots and herbs for medicinal purposes. Amounting almost to folklore, much of this information must have gone back many hundreds of years before Theophrastus put them into writing.

Of the works of Theophrastus, we have today several manuscript copies of two sets of books, both generally believed to be complete: the earlier one, translated into English as "Enquiry into Plants" or as "History of Plants", consists of nine books; the later one, "Causes of Plants", of six books. For the present review the first nine have been seen in German and English translations (Sprengel, 1822; Hort, 1916), and the first book of the "Causes" in an English translation (Dengler, 1927). Information on Theophrastus has also been obtained from Sprengel

(1817), E. H. F. Meyer (1854–1857), Lenz (1859), Jessen (1864), Hoefer (1872), Kirchner (1874), Sachs-Garnsey-Balfour (1906), Hawks and Boulger (1928), Strömberg (1937) and Cohen and Drabkin (1948).

In the " Causes " Theophrastus stated that in both budding and grafting, the ingrafted part uses the other as an ordinary plant uses the ground; budding is really a kind of planting in which the germinating and supporting force is the vital moisture; the bud, having this moisture, is suited to the other part, and the part having the nourishment grows the bud as though it were its own; growth takes place readily because the nourishment is, as it were, predigested. Further on, Theophrastus said that " annual budding "—growth of twigs from the natural buds on the parent plant—is really a sort of second generation, thereby emphasizing the individuality of the twig; and again, " each of the shoots is, as it were, a plant in the tree instead of in the earth ".

This theory of growth, which thus became established in Greek philosophy, lay dormant for many hundreds of years, like most other Greek knowledge. The Romans seem to have passed it by. It appeared again at the beginning of the eighteenth century when Hire (Lahire) (1708) elaborated upon it. Giving credit to " learned philosophers " for the idea, he added that each terminal and lateral bud contains an egg of the species of plant or tree on which it grows. When the egg germinates and grows, it produces a new individual plant of the same species, consisting of a stem which grows into the atmosphere, and a root which grows downward between the bark and wood, as can easily be seen, he says, by cutting into the stem; and in some South American trees it is readily observed that they penetrate the soil.—Was he perhaps thinking of closely appressed lianas?—By their lateral union, the bud-roots of a season form a new layer of wood.

Wolff (1759) believed that bundles grow down from leaves, the stem being a continuation of all united leaf stalks and composed of as many bundles as there are leaves; each leaf, he thought, contains a single bundle. Bundles growing downward from the leaves unite to form a solid cylinder of bundles in the stem. Every year a new additional set of bundles grows downward, each set forming a growth layer. Wolff was apparently unaware of previous literature on the subject.

The noted French botanist and forester, Duhamel du Monceau, considered (1764) that the eye of the bud, as gardeners call it, is a branch in miniature. Each cone of woody growth, he said in the Oelhafen translation (1764), is a separate and distinct tree which has grown over and beyond the similar tree formed during the preceding year.

Erasmus Darwin (1789, 1790, 1800, 1801), who did not state the source of his ideas, went a step farther in that he emphasized the origin of bark, as well as of wood, from bud-roots. A tree is, properly speaking, a family or swarm of buds, each bud being an individual plant, hence truly an annual plant.

On the other hand, the British botanist and horticulturist, Knight (1801), rejected the theory completely.

According to Agardh-Meyer (1831), a theory of bud-roots had been propounded by J. C. F. Meyer (probably 1808).

The most persistent advocate of the theory of descending roots from buds is the French botanist, Louis Marie Aubert Aubert Dupetit-Thouars, whose name is written quite variously in the literature. His theory was apparently first presented in 1805, and again in 1806, 1807, 1809, 1815, 1816 and 1819; of these papers the first and last have not been seen by us. His paper of 1807 has been completely reviewed by Schumann (1873). Dupetit-Thouars believed that a bud originates from a parenchymatous sap and represents a complete embryo; it sends out from its base fibers which grow very rapidly, even with the speed of electricity and light. Every such fiber finds in the mucilaginous moisture between bark and wood an excellent culture medium which stimulates rapid downward growth. Since several fibers grow downward simultaneously, they unite to form a bundle, and they are held together as a bundle in the stem and root. The natural tendency of the fibers to become dispersed and isolated, we are farther told, is not completely fulfilled until they reach the smaller roots, where each fiber becomes a distinct root hair. All buds behave similarly; they make a direct connection between the leaf and the root and grow downward in straight lines; by lateral union they add a new layer of wood to the twig, the branch and the trunk (and presumably to the root also). This can be easily proven by pulling off a bud downward on the stem. New buds are formed each year from the sap. Each of his successive papers adds more de-

tails. He apparently considered his theory to be original with him; yet in other connections, he referred to the works of Theophrastus and of Erasmus Darwin.

This French scientist had a considerable influence on the botanical thought of his day, and we find his version of the bud-root theory repeated, with modifications and additions, by a number of later botanists, even if they were not all convinced of the correctness of his details. According to Sprengel and to M. Agardh, a Prussian lawyer named G. F. Moeller (1751) had propounded a theory like that of Hire; and Linnaeus (Rose, 1775) entertained a similar idea. Willdenow-Link (1821) agreed in part, but asked for more experimentation and proof. Evelyn (1825) cited it briefly, as did Agardh-Meyer (1831). Candolle (1831) leaned toward it.

Poiteau (1831) strenuously called attention to the fact that, instead of being original, as Depetit-Thouars thought, the theory is merely a repetition of that of Hire (1708), whom he strongly defended and whose theory he further elaborated. Candolle (1833a, b) viewed a tree as being composed of as many individuals as there are parts derived from buds. Lindley (1833) held some parts of the theory to be questionable. Reum (1835) considered the root to be a separate and distinct individual. In a later work Link (1837) and Lankester (1840) mentioned the bud-root theory. Meyen (1839) considered a bud to be an individual plant, and Unger (1840) thought of buds and branches as individuals which live parasitically on the mother stem.

The careful work on the cambium by Mohl (1844) and others cast the bud-root theory into the discard in favor of the relation of growth to the physiologic activities of leaves, but there remained some adherents to the older idea until the middle of the nineteenth century (Candolle-Kingdon, 1839-1840; Gaudichaud, 1841, 1852; Theodor Hartig, 1853; Lindley, 1862).

One important phase of the theory, however, has refused to die: the idea of the individuality of buds and branches. Indeed, in a quite recent paper, Murneek (1939) considers that both structurally and physiologically a tree is a " colony " of more or less independent units, the branches.

Thus the idea of the individuality of branches has persisted from the fifth century B.C. to the twentieth, A.D.—a span of 2500 years!

TIP GROWTH FROM THEOPHRASTUS ONWARD

The most obvious aspect of growth, aside from that associated with germination of the seed, is the extension growth which takes place at the tip of each twig. This phenomenon received the attention of Theophrastus (Sprengel, 1822; Hort, 1916; Dengler, 1927; and others) who anticipated some of the more complex problems of growth in length.

Because of a term which has been translated as "budding", there has been some confusion in interpreting Theophrastus' meaning and even in understanding that he was dealing at all with the problem of growth in length. Aside from its use in connection with one type of grafting, the term was used by Theophrastus to mean the formation of a bud, the formation of a cushion below the bud, the opening of a bud, the growth of a bud into a twig, or two or three of these meanings together; and the term "bud" was sometimes used as the equivalent of twig (Sprengel, 1822). Our interest is in those passages in which it refers to the growth of a bud into a twig. There is also some confusion about the term translated as "loosening" or "peeling of the bark", by which Theophrastus seems to have meant that, at certain seasons of the year, man finds it easy to loosen or peel off the bark, not that it does so of its own accord, as it is actually translated. With these interpretations, much of what he wrote about tip growth sounds rather modern.

Opening of the buds and growth of the twigs, he tells us, begin in the spring at such time as the bark can be readily peeled off, that is, with the first sap flow. In Greece such extension growth usually ceases in a few months, whereas in Egypt it may continue for almost the entire calendar year. Trunk and branches grow in length during spring and summer until the leaves fall. Theophrastus believed that extension growth in roots occurs only during the winter months.

A definite season of length growth is further recognized in the statement that trees make their growth all at once or nearly so, whereas herbaceous plants may be seen to grow and flower at any and all seasons of the year.

Trees growing close together grow and increase more in height, and so become unbranched, straight and erect; while those that grow far apart are of greater bulk and denser habit, growing less

straight and with more branches. Reasons are not guessed at, nor are the applications to forestry touched upon.

Terminal bud scale scars and branch whorls are described but not recognized as annual. " The periods of budding can be seen in all trees, but especially in fir and silver-fir, because the joints of these are in a regular series and have the knots at even distances ".

Theophrastus managed to touch upon some very fundamental ideas: the relation of extension growth to the flow of sap and to the presence of leaves, the relation of length growth in the root to that in the stem and of tip growth to diameter growth, and the effect on growth of density of the stand. The influence of climate is also discussed at length. Some of these thoughts have persisted in the minds of botanists well into the nineteenth century, and some are considered today to be fundamentally accurate.

In the days of the Romans very little original work was done in botany. Pliny the Elder seems to have contributed nothing new on tip growth.

Fourteen hundred years later, Leonardo da Vinci (McMurrich, 1930; MacCurdy, 1938) made an unsuccessful effort to determine the age of a branch by its phyllotaxy.

We have been unable to determine who was the first to recognize the fact that in the North Temperate Zone a single tip flush is generally formed in the course of one year, and that its boundary can be determined by the presence of the scars of the terminal bud scales. As common knowledge among foresters and orchardists, the information is perhaps quite old in central and nothern Europe. By the middle of the last century it was quite generally recognized (Wigand, 1854; Schacht, 1860; etc.), although exceptions of several kinds were known even then.

Rees (1929) used the term " primary growth " for tip growth, and called diameter growth " secondary growth ". Various terms have been applied to the single annual tip flush, or to the first flush of several in the case of multiplicity, such as May shoot, spring shoot, summer shoot, first shoot, spring extension growth, and twig extension. A confusing element is introduced by use of the term " internode " for the distance between branches in conifers instead of the distance between leaf bases; in uninodal pines such an internode represents the terminal growth of a year, whereas in multinodal pines it corresponds to the growth of only

a part of the growing season. MacDougal (1939) suggests substituting the term " segment " for such an " internode ". Jacobs (1937) uses the expression " unit of length growth " for the shoot which is derived from a single bud, whether annual or intra-annual. Belief that in pines a single branch whorl is formed in one year goes back at least to Schober (1753).

Attempts were made by Areschoug (1875–1876, 1877) at classifying all types of branches. Pammel (1893) and others distinguished between definite annual growth, which stops when terminal buds are set in the summer, and the indefinite, which continues until stopped by cold weather.

The topic of length growth in roots is of interest because of the long-drawn-out argument, which began with Theophrastus (see above) and Duhamel (1760), as to whether they grow in length during the winter.

Bradley (1716) proposed a very unique theory to account for length growth in roots and stems: vapors are taken in by the roots, passed upwards in the vessels through root and stem to the extremities of the branches, where they meet parts resembling glands; the vapors at the tips of the branches come near the air, are condensed, and return downwards between the four bark layers by means of their own weight, leaving in each bark layer of both stem and root the juices which they need, till at last the more oily part, passing to the root, lengthens its fibers " as icicles are lengthened ". This is only one of many theories to account for the growth of stem and root, which involve refining of the sap.

GROWTH LAYERS AND THEIR ANNUAL CHARACTER

Details of diameter growth, because they are internal and take place on a smaller scale, are much less obvious than are those of growth in length. No written record of diameter growth has been found to antedate the writings of Theophrastus, and his understanding of the process was quite meager. It is true that he discussed the age of some well-known old trees, but their ages were estimated in part from their diameter and in part from " mythological beliefs ". Since many trees are said in his account to grow chiefly or only in the direction of their height, as the silver-fir, date palm and cypress, diameter growth is inferred in others. His knowledge of secondary growth in thickness has indeed, been vari-

ously interpreted. Uzielli (1869) stated that he knew nothing about tree rings; Greene (1909) claimed that he understood the manner of formation of the growth ring; and Green (1914) said that he was acquainted with annual rings and with secondary thickening. Nördlinger (1874) hypothecated that the Greeks were fully aware of the fact that one ring is formed in the stem each year, for they could not have helped but notice, when felling trees, that a thick trunk is made up of many rings and a thin one of but a few; nor could they have failed to guess the relation of rings to age during their abundant work in grafting with one-, two- and three-year-old wood. The truth about Theophrastus, however, lies in the middle ground between these extreme statements, unless the problem is discussed in those books of the "Causes" which we have not seen.

Four aspects of the question of growth layers concern us here. The first is recognition of growth rings as such, regardless of their time or method of formation; the second is their annual character; the third, their structure; the last, their origin.

That growth rings were seen by Theophrastus, there can be no doubt. Rings would seem to be referred to in his statement that round timbers (like those used for masts and yard-arms) have several cores, although his description of these cores leaves some doubt as to his actual meaning. Coniferous wood was probably the most common kind used for such purposes, and mention is frequently made of both Greek fir (*Abies cephalonica*) and silver fir (*A. pectinata*). The present distribution of silver-fir includes the mountains of Greece (Schacht, 1860; Gordon, 1880; Bretzl, 1903), as does also that of *Abies cephalonica* (Dallimore and Jackson, 1923). It is at least possible that the statement above concerning cores refers to the growth rings of these species.

There is, however, much more definite proof that Theophrastus recognized growth layers. We agree with Strömberg (1937) that Theophrastus did not always make a clear distinction between bark and wood, in so far as growth rings are concerned; nevertheless, it is clear to us that he recognized the presence of rings in both bark and wood in at least two species of conifers. In the translations of the "Enquiry" by Sprengel (1822) and by Hort (1916), we find a statement that the bark of the silver-fir has many layers, like an onion; there is always another layer beneath

that which is visible, and the bark is composed of such layers throughout. Sprengel added that the bark of this species does actually occur in layers. One could guess that Theophrastus might have had both bark and wood in mind, and this supposition receives support from a statement a few pages further on, where it is stated that in the Greek fir the arrangement of the rings in the heartwood is " bark-like ". Neither bark rings nor wood rings are specifically mentioned in any other species than the fir and silver-fir, nor are these rings given an annual character. Neither did he mention them as intra-annual layers, that is, as multiple growth layers, two or more of which are formed in the course of a single growing season.

Several important questions arise from this discussion. Why were growth rings mentioned in only two tree species, and those species of conifers? Why were these rings not recognized as annual rings? Why were multiple rings and partial rings not mentioned? These problems have not been touched upon in the voluminous literature on growth layers, except for the suggestions made by Uzielli, Greene, Green and Nördlinger. The answer to some of these questions lies in the geographic location of Greece and in the fact that the foreign botanical connections of Theophrastus lay to the south and southeast of Greece, and not to the north.

It is a well-known fact that, in general, growth layers are most " regular " and " normal " and most sharply defined in the far north and on high mountains (Griggs, 1938; Hustich, 1948; Marr, 1948), and that they become progressively more irregular and more poorly defined toward the tropics, both wet and dry (Penhallow, 1885, 1907; Tschirch, 1889; Antevs, 1917). It is also well known that coniferous trees become progressively fewer as one goes from the north into the tropics, especially in Europe and Asia. Firs and pines belong predominantly in the Temperate Zone. Studies of tree rings do not seem to have been made in Greece since the time of Theophrastus, except for measurements of total diameters by Professor Schmidt on *Populus alba* (Pokorny, 1865–1866). In Anatolia in Asia Minor, however, Gassner and Christiansen-Weniger (1942) find conditions ideal for the study of multiple growth layers, and in Palestine Gindel (1944) and Oppenheimer (1945) find that the Aleppo pine forms

numerous multiple rings. It is a reasonable guess, therefore, that very many of the trees of Greece will be found to show multiple growth layers as well as numerous " irregularities " within these layers, such as lenses and half-lenses. As will be shown further along, Theophrastus found multiple tip flushes in abundance; and while multiple diameter flushes do not necessarily accompany multiple tip flushes, there is a good chance that they very often do, especially in dry tropical and semi-tropical countries. As will be shown later, Theophrastus' knowledge of multiple tip flushes was far in advance of his time, whereas his understanding of growth layers in the wood was decidedly deficient. Again, why?

Closer examination of the situation will bring to light some very interesting comparisons. By far the larger number of botanists who have studied tip and diameter growth in trees have lived and worked in the North Temperate Zone, in which second tip and diameter flushes are the exception rather than the rule, in which growth rings are usually clearly defined and annual in their formation, and in which coniferous trees are very abundant. The home of Theophrastus in Greece lay in a latitude perhaps 400 miles south of that of northern Italy, from which Leonardo da Vinci and later Montaigne reported well-defined annual growth layers; nearly 700 miles below the latitude of Paris; 1000 miles below that of London and Berlin; and still farther from those of Denmark, the Scandinavian countries and Finland, all of which represent later centers of studies in tree growth. Had Theophrastus lived in San Francisco, which has approximately the same latitude as Athens, his writings would have been concerned largely with that area, with Santa Barbara (corresponding to the Island of Crete) and with a large portion of northwestern Mexico (the equivalent in latitude with Memphis at the apex of the Nile delta). There is mention in Theophrastus of the flora of the mountains in Greece and Crete, which brought him into contact with some of the northern forms, especially with the fir and silver-fir; but he seems to have known very little of the world to his north and northwest. That unknown world, containing the centers of future research on tree growth, has the following rough latitudinal equivalents on the west coast of North America: Pisa in northern Italy with the California-Oregon boundary; Paris with the United States-Canadian boundary; London with the northern

end of Vancouver Island; Berlin with the middle of British Columbia; Oslo, Uppsala and Helsinki with the northern end of the Alaska panhandle. Indeed, Theophrastus almost lived in a world apart from the rest of Europe, not only geographically but in the sense of tree growth as well. Many plants of southern Europe, as the olive and the oleander, have very indistinct rings (Sanio, 1863; Müller, 1888; Dallimore and Jackson, 1923; a series of articles on the region of Bari, in southern Italy, beginning with Giannuoli, 1947). This must be even more true of Greece, Crete and Egypt.

It is little wonder, then, that Theophrastus mentioned growth rings in only two species, the Greek fir and the silver-fir, both of which are more northern coniferous trees found in Greece near the southern limit of their ranges, and there only in the higher mountains. One cannot agree with the suggestion made by Nördlinger (1874) that the Greeks must have known that growth rings are annual; indeed, we can safely infer that Theophrastus must have had such an abundance of multiple rings on hand that he did not recognize the annual character of any of the rings.

We have now answered the first two of our problems concerning growth layers. The third, dealing with their structure, is more difficult to solve. Theophrastus divided the stem into pith, wood and bark, as is still commonly done today. The grain of wood is mentioned on numerous pages, and this of course refers directly to ring and ray structure. He tells us that, as compared with trees growing close together, those growing far apart have harder wood and closer grain. In other cases grain and rings are inferred; thus the best timber came from Macedonia where it grew in the mountains—best, no doubt, because it was close-grained.

Recognition of growth rings implies recognition of early and late wood. The statement above on harder wood can mean nothing else than a larger proportion of late wood, and closer grain must mean thinner rings. That thin rings have a larger proportion of late wood has been abundantly proven by Schacht (1853) and others. Theophrastus also occasionally mentioned the density of wood, a closely related problem.

There is a large body of literature on the best season for felling trees. In the United States, where logs are stored in the water of

mill ponds, the problem seems not to concern us.   But where freshly cut timber is stored on the ground before being sawed into lumber, there is often a real problem of rapid fungous decay.   A recent very extensive work by Gäumann (1930) in Switzerland shows that timber cut in the spring when the sapwood is very wet will decay much more rapidly than that cut in autumn or winter after the drier late wood has been laid down.

This problem, too, seems to have begun with Theophrastus. Round timbers (for masts, etc.) should be cut in the spring when the tree is coming into leaf, for then the bark strips easily.   Other trees, he says, especially those timbers which are for underground use, are cut in September or some time after the wheat harvest; among these, mention is made of oak, elm, maple, ash, beech and lime (*Tilia*).   Oak is cut latest of all, in early winter or at the end of autumn; if it is cut at the time of peeling, it rots almost more quickly than at any other time, whether it has bark on it or not; this is especially so if it is cut during the first peeling, less so during the second, and least during the third.   Again, wood is stronger if cut after ripening of the fruit.—It should be clear from these examples that Theophrastus had a fair concept of early and late wood, even though he nowhere directly discussed the parts of a growth ring.

The fourth problem of growth layers, that of their origin, is scarcely touched upon by Theophrastus who knew however, that growth takes place in both bark and wood.   In some trees, he says, as cork oak, cherry and *Platanus*, new bark is said to form under the old bark which withers and cracks and may fall away of its own accord; there is no suggestion at all about the origin of the wood.   The cambium layer is very dimly anticipated in his knowledge that the bark peels off easily when the tree is in sap, because there is a fluid under the bark.   Many hundred years later this fluid itself was called the " cambium ", was believed to give rise to the bark, and the latter in turn to the wood; these Renaissance ideas may easily have been derived directly from Theophrastus.

The later scientists of Greece and of Alexandria, Egypt, are said to have followed the botany of Theophrastus rather closely and to have developed little or nothing that was new.

Pliny the Elder (c. 23–79 A.D.) appears to have been the only Roman to write extensively on trees.   Of his 37 books on natural

history, Books 12 to 21 treat of trees, plants and flowers. These have been studied in the Bostock and Riley translation (1855–1856). The comments of Stone (1921), Hawks and Boulger (1928), and of Ugrenović (1938) have also been seen.

Pliny lived in northern Italy much of his life and should there-fore have been able to study a greater number of trees which are typical of the North Temperate Zone than was Theophrastus. But he was so busy compiling his 37 books on natural history from some 2000 different Roman and foreign writings that he had little time for original observation. What these writings were and what they may have contained on the growth of trees will forever remain a mystery, for Pliny seems not to have been much inter-ested in the subject. He himself contributed very little new ma-terial other than a description of the very fancy types of grain in some very valuable tables whose large tops were made of citrus wood. He discussed the age of some old trees, but not from growth layers; trees from certain localities, such as the mountains, are of the highest quality—no reason is given; and early and late wood are noted in dicotyledonous wood, for they constitute light and dark zones. The bark of the cork tree is remarkably thick, and if removed it will grow again. Some of these statements are actually less detailed than the corresponding statements in Theo-phrastus.

The following very interesting statement is taken from Hawks and Boulger (1928): " When, about A.D. 850, the Caliph Mote-wekkil cut down all the sacred Cypresses of the Magians, this one is said to have shown 1450 annual rings of growth ". Further details, which would be so interesting and illuminating, are lacking.

Growth layers are apparently not again mentioned in botanical literature until the thirteenth century. Albertus Magnus (?1193–1280), also known as Albert von Bollstädt, mentioned ring-like layers of wood in the alder (Hawks and Boulger, 1928); his con-cept of rings in general was not the same, however, as is ours to-day, for he seems to have considered the structures to be rings only if the rays are not so broad as to be seen with the unaided eye before the wood (E. H. F. Meyer, 1857).

Recognition of the annual character of growth rings in northern Italy by Leonardo da Vinci and later by Montaigne has been fre-quently noted (Glock, 1941). Leonardo (Uzielli, 1869; Toni,

1922; McMurrich, 1930; Baldacci, 1940) no doubt worked out the problem independently; Montaigne (Dédéyan, edition 1946) got his information from artisans who worked with wood. In both cases the knowledge came from northern Italy, where no doubt most of the trees used had been cut in the mountains, the alps and the Apennines, in which growth layers are known to be prominently bounded and to be largely annual in character. It would appear very likely, indeed, that the knowledge of the engineer, Leonardo, was passed on in his own time to the wood industry which, some 80 years later, transmitted it to Montaigne. Both Leonardo and Montaigne also dealt with the problem of eccentricity in the trunk.

With these two writers and the knowledge harbored by Italian artisans, the annual character of growth rings in trees should have become well established in the minds of botanists; but such is not the case. The post-Renaissance botanist was a taxonomist who looked down his nose at things anatomical. Furthermore, Leonardo's botanical writings remained unknown until less than a century ago, and Montaigne's reference to growth rings was discovered by botanists only a short time before that. And again, the layman's knowledge is all too often ignored by the scientist. It was, therefore, necessary to rediscover the fact that growth rings in the wood are annual in character.

Credit for this rediscovery is generally given to the plant anatomists Malpighi (Möbius, 1675, 1679) and Grew (1682). Malpighi's work marked the third time for this discovery in Italy. These two botanists, mainly interested in the anatomy of individual cells, contributed very little to their organization into growth rings, in so far as found in the books available to me.

At about the same time there appeared some first class completely forgotten work on " tree rings " by the Dutch microscopist Anton van Leeuwenhoek; exact dates have not yet been checked, and hence priority not established between Malpighi, Grew and Leeuwenhoek. It is unfortunate that the latter has of recent years been pictured merely as a hunter of curious odds and ends, for this does grave injustice to some of his work, especially that on plant anatomy (compare the estimates of Sachs, 1906, and Jessen, 1864). The details and accuracy of his beautiful drawings of cross sections of wood, made by a professional artist, as reprinted

in Hoole (1816), would do credit to a modern textbook in plant anatomy. Their written descriptions, also excellent, repeat several times that each circle in the wood of a tree undoubtedly marks the increase in growth of a single year.

Doubts of the annual character of rings, which persisted in central Europe, were partially laid at rest by Schober (1753) who showed that in a pine tree known to be 22 years old, the number of rings agreed with the number of branch whorls at the 5th, 10th, 15th and 20th whorls. He admitted, however, that he had seen a few thin rings in the Carpathians which may not have been annual, and he suggested that further proof of the annual character of rings could be obtained by counting the number of rings formed, since certain " monuments " (inscriptions?) had been left on trees by hunters.

According to Goeppert (1868), who did not mention Schober, a number of people, beginning about the middle of the seventeenth century, were able to prove the annual character of growth rings by the study of " monuments " and dated inscriptions in trees; the number of years which had elapsed since the inscription was cut corresponds with the number of growth layers which had overgrown the inscription.

Soon, however, the annual character of rings became very widely accepted in Europe, as is attested by the works of Linnaeus (Holmboe, 1910), Duhamel du Monceau (Oelhafen, translation 1764), Winterfeld (1791), Medicus (1799), Kieser (1812), Willdenow-Link (1821), Evelyn (1825), Candolle (1827, 1831), Agardh-Meyer (1831), Reum (1835), Dutrochet (1837), Link (1837) and Meyen (1837). Of these, we find some reservations or doubts only in Winterfeld, Evelyn and Agardh-Meyer. All of this seems to have established firmly the principle that the age of a tree can be determined by the simple process of counting its rings.

ANATOMY AND CLASSIFICATION OF GROWTH LAYERS

Two adjacent growth layers, in order to be recognized, must be separated by a distinguishable boundary between them. In the Temperate Zone this usually becomes a matter of establishing the differences between early and late wood, or differences in the distribution or size of vessels. In simpler cases this is so obvious

that it was evident to the Greeks, the Romans, to Leonardo da Vinci, Montaigne, Malpighi, Grew and Leeuwenhoek, as previously stated.

Leeuwenhoek (Hoole, 1816) gave excellent written descriptions and detailed figures, as seen with his microscopes, of the growth rings of fir, oak, elm, beech, willow and alder, describing accurately the differences between the wood laid down during spring and that toward autumn. A piece of ebony wood from Mauritius is described as being without rings because it grew in a tropical climate. Rings are also absent, he wrote, from boxwood; no explanation is offered. His breadth of view is shown by the fact that he selected representatives of conifers, ring-porous species, diffuse-porous trees and trees in which boundaries are absent. Although no terms are applied to the ring types involved, each type is clearly and accurately described and depicted, and its late wood distinguished from the early.

It is surprising that such a clear understanding of the two major parts of a growth layer were followed by a marked deterioration in the knowledge of growth layer anatomy. John Hill (1770), who had at his disposal a good compound microscope, shows several drawings of cross sections of branches of English trees from pith to bark, with considerable detail of structure. But —a fact which does not seem to have been noted in the literature —he has some of his rings backwards, the outermost part of some of the layers containing the larger and more numerous vessels! Medicus (1799) was not certain of the cause but thought that the shaded appearance in the outer portion of a ring might have indicated denser tissue caused by thicker fibers. Microscopes were apparently not yet in general use. Kieser (1812), who must have had a microscope of some sort, did better, for he tells us that the larger vessels in a ring occur nearer the pith and are formed in the spring; the smaller ones are formed in autumn and occur in that part of the ring nearer the bark; this is correctly shown in several of his figures, but his Fig. 86, a cross section of the stem of *Rhus typhina,* is apparently copied from Hill and shows the reverse position of early and late wood.

Beginning with Evelyn (1825), rings are generally described with accuracy and the relation of the parts reasonably well understood. Agardh-Meyer (1831) tells us that some writers

(Sprengel, Dutrochet, Candolle) add a third layer to the typical early and late wood, a layer composed of thin-walled cells which bounds every ring on the inside.

The two major parts of a ring, at first merely described and not named, were soon called " spring " and " autumn wood ", it being generally believed that the cambium remains active well into the autumn and even into the winter. And when it became known that the late wood is formed during summer, we find the older term retained for many decades (Schacht, 1853; Haberlandt, 1884; Wiesner, 1898; Benecke and Jost, 1923; and wood technologists in general). The term " summer wood ", however, gained slowly in favor.

A new concept entered the picture when R. Hartig (1888) divided the ring of a coniferous tree into three zones: a spring zone, laid down in April and May, a summer zone of May and June, and an autumn zone; sharp boundaries between these are not always present, any more than between the older spring and autumn woods. The intermediate layer was accepted by Strasburger (1891) who gave it the name " Folgeholz " (ensuing or subsequent wood). Janssonius (1906–1908) used the terms " early wood ", " middle layer " and " late wood ". The terms " early " and " late wood " are used today for the two commonly recognized parts of the growth layer, in both coniferous and broad-leaved trees; these time terms have an advantage over " spring " and " summer wood " which are also time terms, in that they are properly applicable to the parts of multiple rings. The purely anatomical designations " light wood " and " dense wood " have been suggested.

Under unusual conditions a ring may be composed of a single part. Schacht (1856) showed that in wet moor soils *Pinus silvestris* forms only spring wood in its broad rings. When ring boundaries are absent, as in many of the trees of the tropics, only spring wood cells may be formed. It often happens, after insect or frost injury, that a growth layer may contain only late wood, the early wood being wholly absent. Lenses are often found to contain only late wood at their cusps.

Several botanists have been led astray by the primary xylem. Since a clear distinction was not made between the meristematic cells near the tip of the stem (cambium ring) and those in the

true cambium until about a hundred years ago, there could of course be no distinction between the primary and secondary xylem. The primary xylem was recognized as a distinct region by John Hill (1770) who called it the "corona". This zone was believed by Hill, Link (1807), Hundeshagen (1829) and again Link (1837) to be a ring of bundles laid down somehow after the first true ring has been formed, between the latter and the pith.

The presence of reaction (compression) wood within a growth ring does not often cause confusion, but there have been instances in which it was mistaken for late wood.

A variety of methods of classifying the growth layers of "normal" Temperate Zone trees has been proposed. The oldest is a division into those of gymnospermous trees (without vessels, in our modern sense) and broad-leaved or dicotyledonous trees (with vessels). This seems to hold in all but two instances: (a) vessels are present in the advanced gymnospermous order Gnetales, containing the three genera *Ephedra, Gnetum* and *Welwitschia*; (b) a few primitive dicotyledonous families, e.g., the Winteraceae (I. W. Bailey, 1944), are completely without vessels. The dicotyledonous group has been very commonly further subdivided into ring-porous and diffuse-porous species, depending on the distribution of the vessels; in the Temperate Zone these two subdivisions are rather sharply separated, one from the other, while in the tropics there are many intermediate conditions. Janssonius (1906–1908) found several tropical trees to show vessels mainly in the middle of the growth ring, whereas in others the middle had the fewest vessels. Chowdhury (1939b) also reports that a zone of vessels may be present only in the middle of the diameter increment.

Tiemann (1942) prefers very simple terminology for the two broad-leaved groups: woods in which pores vary in size from early to late wood, and woods in which pores are uniform in size throughout the ring.

There are very many more diffuse-porous species than there are ring-porous, even in the North Temperate Zone. Jeffrey (1917) considered the ring-porous condition to be uncommon at high latitudes and rare in the tropics, and Chowdhury (1939 a) states that nearly all dicotyledonous trees of India are diffuse-porous. The significance and the geographic distribution of ring-

porous and of diffuse-porous species was further discussed by Simon (1902), Antevs (1917), B. Huber (1935), and by Ladefoged (1952).

The cause of the differences between ring-porous and diffuse-porous woods has from time to time been sought in climatic or soil factors, operating either directly or indirectly; these are of course not true causes but, instead, influencing factors. According to B. Huber (1935), ring-porous woods have a biological advantage over diffuse-porous species, and the former are more plentiful in drier habitats. Simon (1902), working in the tropics, believed that the ring-porous condition is associated with the sudden development of leaves in spring. B. Huber (1935) shows that in ring-porous woods the transpiration current moves upwards about ten times as rapidly as in diffuse-porous species. This is true in spite of the fact that in ring-porous wood the water passes upwards only in the latest-formed growth ring (Rumbold, 1920; B. Huber, 1935), whereas in diffuse-porous species several rings of the sapwood are involved in upward conduction (B. Huber, 1935). Huber relates this apparent anomaly with the greater diameter and greater length of the vessels in ring-porous species.

Very important work on the growth of trees in the spring has been done by the " strip " method (Priestley, Scott and Malins, 1933). As the cambium swells in the spring, the bark slips easily over the wood, and a separation takes place in the plane of the cambium. For a time, all or nearly all of the new cells derived from the cambium are formed on its inner face; hence, when the bark is peeled off in this stage, the newly formed tissue is left as a soft layer overlying the lignified wood of the previous season. This can then be scraped off in long strips by means of a small knife or a screwdriver. The strips can be floated out in water and are very suitable objects for microscopic study. The cells are so plastic that they seem little injured, cytoplasmic streaming having been observed in some water mounts. The method is less effective after enough radial growth has occurred to make the strips too thick for examination; however, they can then still be obtained for a time by scraping the inside of the bark. The strips can be examined under the microscope either in water mounts or as fixed, stained and permanently mounted slides. By 1933 the strip

method had been used successfully on some 30 species of hardwoods and six of softwoods. It is again described in later papers (Priestley, 1935; Priestley, Scott and Malins, 1935; Priestley and Scott, 1938).

The method is much more rapid than any previously known for the study of the cambial activity of trees. A good deal of previous work has been corroborated with its use, especially on the time of beginning of cambial activity, on its basal progression (R. Hartig, 1894a) and on the length of individual vessels. Cambial activity begins much earlier in ring-porous than in diffuse-porous trees; it also progresses downwards from the buds to the roots much more rapidly, and the individual vessels are very much longer than in the diffuse-porous species.

A correlation has been attempted between the type of porosity and the evergreen habit in dicotyledonous trees. Simon (1902) found that in the evergreen species of the tropics the conducting tissues are rather evenly distributed throughout the growth ring and that they function for a long time; in deciduous species, on the other hand, conducting tissue is composed of larger cells chiefly in the spring wood, and their functional period is shorter. Working in India, Chowdhury (1939a), however, detected no correlation between the sharpness of the growth ring boundary and the evergreen habit, nor (1939b) between the evergreen habit and the presence or absence of growth ring boundaries. B. Huber (1935), working in central Europe, states that deciduous oaks are ring-porous whereas evergreen species of the genus are diffuse-porous.

The various facts here mentioned have led to speculation as to the significance of the ring-porous condition. The work of B. Huber (1935) emphasizes the highly specialized character of the pore zone in ring-porous woods. Chalk (1937) goes a step further and suggests that the ring-porous condition is completely distinct from and in no way related to the diffuse-porous condition; his point of view is that (a) the late or summer wood of ring-porous species is the equivalent of the entire ring of diffuse-porous species, (b) the pore zone in ring-porous trees represents an additional highly specialized tissue which has no equivalent in diffuse-porous woods, and (c) the term "early wood" should imply early development in relation to the foliage rather than to its posi-

tion in the growth ring and should be limited to softwoods (conifers) and to ring-porous hardwoods.   In a later paper, Chalk (1937), after stating that for practical purposes it is often sufficient to speak of the inner and outer parts of a ring, suggests the following equivalents:

Conifers	Ring-porous species	Diffuse-porous species
———————	pore zone	———————
	"early" wood	———————
early wood	"late" wood	entire ring
late wood		(1) inner part
		(2) outer part

There has been some speculation on the origin of ring-porosity. B. Huber (1935) considers that the diffuse-porous condition is the older and that the ring-porous arose from it by an increase in the diameter of the vessels.   The same conclusion has been reached in part by Gilbert (1940) from a study of the first growth ring of the stem, of the rings of seedlings, and of the " reversion " from the ring-porous to the diffuse-porous condition following wounding of the adult wood of *Quercus*.   He considers ring-porosity to be more advanced from an evolutionary point of view; it has developed from diffuse-porosity as a response to climatic conditions characteristic of the North Temperate Zone.   Chowdhury (1953) discussed the role of initial parenchyma in the transformations of diffuse-porous to ring-porous structures.

A complete classification of the types of growth layers has been only rarely attempted.   One such effort is that of Geiger (1915) for teak in Java: (*a*) entire, " closed " annual rings; (*b*) partial, closed " annual " rings; and (*c*) intermediate [intra-annual] rings, which in turn may be entire and closed, partial and closed, or merely color rings [late wood layers of darker color].

In work with growth layers it is often necessary to know when the cambium begins its activity and when such activity ceases.   A variety of methods has been devised for making such determinations, including diameter measurements with steel calipers, circumference measurements with steel tapes, increment borers, circumference measurements with various types of dendrometers, and dendrographs, and the " strip " method; summaries of methods are found in Antevs (1917), Büsgen-Münch-Thomson (1929) and MacDougal (1938).   The recording of measurements

of circumference, diameter, or of the thickness of individual rings began, it appears, in the middle of the eighteenth century. Duhamel (1758) used a fine brass wire and also a fine copper wire for the measurements of the circumference of various trees, even going so far as to show that expansion and contraction of the wire with changes of temperature were too small to affect his results. Other early recorders were Marsham (1759), Winterfeld (1791), South (1792), Reventlow (preceding 1828, published 1934), Candolle (1831) and Hall (1839).

The most commonly used methods, however, of studying the details of cambial activity involve microscopic examination of a bit of tissue including the cambium, which may be obtained in any one of various ways. Interpretation always depends upon the number of rows of new cells formed and on a set of anatomical characteristics of the cambium region and of the tissues recently formed by the cambium. The most frequently used criteria are the radial dimensions of cambial and derivative cells, thickness of the cell walls, and the amount of lignification in these walls (Lodewick, 1928; MacDougal, 1938; and many others).

Wight (1933) feels that these criteria are not satisfactory; he proposes and uses in a study of cambial activity of *Pinus sylvestris* a complicated set of criteria which may be summarized as follows:

a) When the cambium is at complete rest, its radial walls are thick, its tangential walls have a uniform thickness, and the entire cambial zone is narrow and has a geometrical and almost solid appearance.

b) When the cambium begins activity, the cells of the cambial zone swell up and some of them differentiate directly without previous cell division.

c) When the cambium is in a stage of active cell division, there is a loss of regularity in the cambial zone, the radial walls of the cambial cells are still thick while its tangential walls are thin, and soon there is a smooth transition from the narrow cambial elements to the newly completed and completely differentiated tracheids.

d) When the cambium ceases to divide, the cambial zone again becomes narrow; next to it will occur a row of cells showing only little radial expansion; and next inward a zone of only partially

differentiated, somewhat thick-walled tracheids. Lignification is slowed down, the outer tangential wall being the last to lignify.

e) When a second period of diameter growth begins before lignification is complete, the situation can be recognized by the fact that lignification commences at once in the freshly formed tracheids.

Such a complete set of criteria for determining cambial activity has not been worked out for other trees. Details will certainly be found to differ somewhat from species to species, especially in the broad-leaved trees as compared with *Pinus sylvestris*.

MULTIPLICITY IN TIP GROWTH

It has long been considered " normal " for a tree, shrub or herb to make its total growth in length for a year in a single spurt which shows the typical sigmoid curve of growth; the single resulting tip flush reaches maximum length without intervening rest periods, and when it has completed its extension growth, a long rest period follows which lasts until the beginning of the growing season of the ensuing year. Such does in fact commonly take place in the North Temperate Zone, where most of the studies on tree growth have been made. But it is not the universal rule even there, for various trees, or individual twigs on a given tree, may show two or more periods of extension growth in a single year, alternating with more or less well-defined periods of growth inactivity.

The history of our knowledge of such multiple or intraseasonal tip flushes, like that of so many of our botanical problems, goes back to the Greeks. Theophrastus considered multiple tip flushes exceptional in Greece, for he wrote (Hort, 1916): " Now most trees, when they have once begun to bud, make their budding and their growth continuously . . .". Nevertheless, he devoted so much more space to multiplicity of tip growth that one wonders whether such phenomena were not so well known in his day as almost to amount to folklore. Continuing the interrupted quotation above: ". . . but with fir, silver-fir, and oak there are intervals. They make three fresh starts in growth and produce three separate sets of buds ". At least in the oak, these periods occur in May, June and July. On rare occasions there is in some trees a fourth growth from buds in September; such is more common

on the Island of Crete.   And in Egypt there may be no cessation at all of twig growth, or the process may be suspended for only a short time.

The trees involved in the account of Theophrastus are both native and cultivated, both coniferous and broad-leaved.   He described the supplementary flushes as being of two kinds, end-on-end from terminal buds (up to four in a series), and lateral growths from lateral buds.   Mention is also made of second, third and fourth flowering and fruiting periods.

In dealing with the factors or causes of such multiplicity, Theophrastus was of necessity rather vague.   The time of beginning of each tip growth is always associated with an increased sap flow, of which there are three or four, and with a period of easy peeling of the bark.   Sprengel (1817) wrote of an old Greek maxim to the effect that the sap rises and the bark can be peeled three times a year.   Theophrastus called the growth of a bud a sort of birth, and spoke of the phenomenon of additional growing periods as super-budding and super-germination; this was, of course, in line with his idea of bud-roots, previously discussed.

The two supplementary growth periods of summer are associated by him with the second and third sap flows, hence with a greater amount of moisture in the plant at those times.   That of September is related to a healthy, vigorous plant, a good soil, and a long autumn with favorable growing weather and mild air.   Still another recognized cause is defoliation: an olive tree, whose young shoots had been eaten off by locusts, grew again.

All in all, Theophrastus touched upon almost all modern aspects of multiple tip growth; even the background for their relation to hormones was very dimly anticipated; for, he says, if one permits the buds to remain on trees, the latter grow rapidly in length, but if they are removed early, the trees become shorter and more compact.

Multiple tip flushes were passed by completely by Pliny, except for mention of second and third flowering and fruiting periods in a single year in some orchard trees.

After the Romans the problem of multiplicity in tip growth was not again considered scientifically for hundreds of years. Simple observations must have been numerous on both second tip flushes and second periods of flowering and fruiting.   For in-

stance, Kobel (1931) says that second tip flushes have been known in fruit trees since olden times. Scientific study of these phenomena, however, seems to have begun again with Duhamel (1758), Borkhausen (1800), Saussure (Vaucher, 1822) and Sénébier (8, i.e., 1800). Burgsdorf (1783–1800) considered second tip flushes normal and common in the oak.

During those early years, when meristematic tissues were unknown, all growth was attributed directly to the sap. The terms " May sap " and " spring sap " became almost synonymous with the first tip flush, and " August sap " with the second. In Germany the second flush is commonly called " Johannistrieb " (St. John's shoot) because of its unusual time of formation; in England, " Lammas shoot " for the same reason; in France, " l'été de Saint-Martin " and " sève d'août ". Other terminology which has been used is " second bud ", " August bud ", " repeated formation of buds ", " August sap ", " autumn sap ", " second shoot ", " summer shoot ", " repetition of shoots ", " second sprouting ", " repeated sprouting ", " anomalous sprouting ", " midsummer growth ", " late-season growth ", " secondary growth ", " secondary elongation ", " secondary elongation growth ", " midsummer secondary elongation ", " post-seasonal growth " and " secondary leafage "; and for the first and second shoots combined, " double shoot " and " double header ". There are also many papers on the topic of " summer rest ". The very fact that such a multitude of terms has been used is in itself proof that the phenomenon is anything but rare.

The types of second tip flushes were classified by Areschoug (1875–1876), by Ratzeburg (1868) and by Späth (1912); the latter (1912, 1913) has given us the nearest complete discussion in the literature of second tip flushes.

During the nineteenth century second tip flushes were discussed very extensively in Germany, Switzerland, France, England and Sweden, and in the twentieth century the United States and many other countries were added to the expanding list. Phases of the problem considered are mere recognition, abundance, species involved, the many types of tip flushes and their description, time of formation, number per year, influencing factors and causes, and artificial induction and suppression. The topic is indeed too huge to be summarized here in all of its phases.

Various factors and causes have been associated with the formation of second tip flushes. Many types of external factors have been invoked (Duhamel, 1758; A. Fischer, 1891). Unusual weather conditions are cited by Vaucher (1822), Nördlinger (1874) and Areschoug (1875–1876). Perhaps the most common of the external factors considered is temporary summer drought (Theophrastus; Agardh, 1832; Döbner, 1865; Schumann, 1873; Magnus, 1874; Nördlinger, 1874; Ward, 1892). Strong light is mentioned by Döbner (1865) and by Lakon (1915); defoliation by insects during the spring is proven responsible for substitution flushes by Döbner (1865), Ratzeburg (1868), Nördlinger (1874), R. Hartig (1892a) and many others; injury by rodents, by Ratzeburg (1868); damage by frost, by a host of workers; defoliation by storms, by Schrenk (1898). In nearly all cases the relation to newly formed leaves was noted.

It may be added parenthetically that the word "climate" is very often misused. Correctly applied, it of course means a composite or generalization of weather conditions throughout the year, averaged over a series of years. The term is altogether too often made to substitute for the state of the atmosphere at a given time, which is of course weather. Second tip flushes have been associated with both climate and weather.

An almost equal number of internal factors has been held responsible for second tip flushes (J. Huber, 1898), the oldest of which is renewal of sap flow by Burgsdorf (1783), Borkhausen (1800), Senft (1857) and Döbner (1865). The food accumulated and stored in late summer and autumn is largely used up by the growth of spring; accumulation of new food during spring was considered responsible for the second tip flush by Roemer (1806), Th. Hartig (1837b), Schacht (1860) and R. Hartig (1891). Earlier the "physiological action" of mature leaves was invoked by Hartig and Hartig (1836). And premature opening of the first set of buds was named by Candolle (1832). Increased water content in the tissues was considered by Hundeshagen (1829) and by Willdenow-Link (1821). Hundeshagen (1829) further considered the stimulating action of sap flow as a possibility.

It is of considerable interest that, long before heredity was at all understood, the capacity to form second tip flushes was regarded as inherent by Saussure (Vaucher, 1822), Sénébier (8, i.e.,

1800), Sprengel (1802), Candolle (1833a), Areschoug (1875–1876), Jost (1892) and Ward (1892).

The literature since 1900 for the most part follows the same pattern. The topic is well summarized in Büsgen-Münch-Thomson (1929), in other editions of Büsgen's excellent book on the growth of trees, and in Antevs (1917).

An interesting sidelight on heredity has been developed by comparison of second tip flushes with the growth of tropical trees. Magnus (1913) suggests that the central European beech and oaks develop second tip flushes because to do so is a matter of inheritance from evergreen ancestors, the periodicity of which did not coincide with the present European climate; the present beech and oaks have not yet adjusted themselves to the change in climate. Büsgen (1917) considers this possible but adds that the trees are nevertheless subject to modifications by external factors. J. Huber (1898), working with the periodic phenomena of the rubber tree (*Hevea brasiliensis*) considered the possibility that, in its original home, this species had adapted itself to several rainy seasons each year, and that this tendency has continued in its new home in the Hylaea in Brazil.

MacDougal (1938) suggests that second tip flushes will probably be found to depend upon the factors affecting the formation or disintegration of growth-promoting substances. The relation of growth hormones to second tip flushes is apparently an open field for research.

MULTIPLICITY IN DIAMETER GROWTH

Two thousand years were to pass between the time that growth rings in trees were first mentioned by Theophrastus and general acceptance by botanists of their annual character. The works of Leonardo da Vinci, Montaigne and Albertus Magnus were not known to botanists until the nineteenth century and consequently exerted no influence on botanical thought. Plant anatomy had its beginning as a science with the work of Malpighi, Grew and Leeuwenhoek in the latter part of the seventeenth and the early eighteenth centuries, and it was these three men who succeeded in establishing among botanists the fact that a single growth ring is formed each year. To them, then, goes the doubtful honor of establishing firmly the truth of that which is not necessarily true.

It must have been quite disconcerting to the botanist to dis-

cover that growth rings are not always annual, that indeed two or more layers may be formed during a single growing season. It has been shown in a previous section that Theophrastus must have come face to face with the problem of multiplicity of growth rings without recognizing it at all. Pliny and Albertus Magnus seem to have been ignorant of it. It must have been questioned before the days of the three plant anatomists mentioned above. And there were always some doubting Thomases, particularly in France, England and Germany. Perhaps the first clear statement of multiplicity appears in the writing of Duhamel (1758) who observed in France that trees known to be 20 years old did not always have 20 rings; that trees ten years of age sometimes had more than ten rings. This bombshell (for Duhamel was widely read, both in French and in translation) must have had its influence on a number of botanists, for we soon find recognition of multiple growth rings by John Hill (1770), Mirbel (1802), Sprengel (1802), Cotta (1806), Link (1807), J. J. P. Moldenhawer (1812), J. E. Smith (1814), Willdenow-Link (1821), Candolle (1833a, b), Reum (1835), Treviranus (1835), Bischoff (1836), Nördlinger and Poirson (1845) and a large number of other botanists to the present day.

Such heresy could not be accepted without strenuous opposition, especially in Germany where the science of forestry was developing rapidly. Burgsdorf, although describing the second tip flush of beech (1783) and considering second tip flushes both normal and very common in oak (1787), nevertheless stoutly denied even the possibility of the existence of second diameter flushes. The age of a tree can be definitely determined, he wrote (1788), by counting the number of wood rings: " This truth can be questioned only by simple-minded people who have no fundamental knowledge ". Meyen (1837) stated that multiple rings are not possible, except perhaps in certain wet tropical regions with two harvests, summer and winter; they are not at all possible in most tropical regions. Theodor Hartig, who (1837b) had stated that the second growth ring might easily be mistaken for an annual ring, later (1860) doubted the existence of double rings; he had seen no cases of what looked like doubles to the unaided eye which a simple handlens could not refute. Wiesner (1890) claimed that all growth rings in Germany are sharp and distinct.

And in this country, the German-trained Fernow (1887, 1888, 1897), while begrudgingly admitting some difficulties in the determination of annual rings, was firmly convinced that the annual boundary can always be recognized; that the finding of multiple rings, common in the United States at that time, was in part merely a prejudice against the accepted theory, or a love of new discoveries, or a lack of sharp observation.—The letter of the law must be upheld at any cost!

Statements on the abundance of multiple rings vary widely, even when their presence is recognized. On the one extreme are the beliefs that they are very rare, occur in Europe in only a few species, and are always readily distinguishable from true annual growth rings. On the other extreme, John Hill (1770) was convinced that it is normal for two growth layers to be formed each year in all trees of England, one in spring, the other soon after midsummer. And Bechstein (1821) believed that double rings are found in nearly all German species of woody plants. Their presence in conifers was long denied, later abundantly substantiated. All of this refers to their "natural" occurrence; their formation after severe injuries, such as defoliation by insects, is accepted by all workers in the field.

Methods of studying multiplicity are several and varied. A simple observation that a branch on a tree has grown to a certain length during a season, and then examining cross sections at the base of the branch, is of questionable accuracy, even though often correct. R. Hartig (1869) thought he had a fool-proof method, one already used by Schober (1753), when he compared the number of rings at different elevations of young trees of *Pinus strobus* with the number of branch whorls, since up to that time it was not questioned that a single branch whorl is formed each year. In more recent times, however, many workers have shown that a number of species of pine may develop two whorls of branches in a single growing season. The same objection holds for comparing growth layers with the counts of terminal bud scale scars, for, as already shown, tip flushes are often multiple.

A method which has been used very extensively in older tree trunks is to follow a questionable ring completely around the circumference. This procedure will no doubt eliminate some double rings, but is by no means perfect.

Aside from the use of internal markers, to be discussed later, only one accurate method is known to us: placing definite marks at known points along a branch with a nail, notch, string or paint, and measuring the branches at the end of the growing season or at intervals. Thus Kny (1879), who wrote the first comprehensive paper on double rings, stressed the necessity of studying branches of known age. And Schrenk (1898) stated that ". . . in determining the age only a personal knowledge of the twig is to be considered ".

Many terms have been applied to the rings of a multiple series, the most common being " double rings " or the anomalous term " double annual ring " for a series of two, and " false ring " or " false annual ring " for the second of such a series. The word " double " is also used for the outer ring of a pair, in the same sense as the double of a double rainbow. Among the many terms which have been gleaned from a large body of literature for multiple rings, we may mention the following:

summer ring
summer layer
accessory layer
summer follow-ring
St. John's ring
spring wood in the autumn wood zone
false early wood
fictitious ring
spurious ring
false ring
extra ring
superfluous ring
supernumerary ring
non-annual ring
quasi-circle
double rings
the double ring or simply the double
duplicate rings
triplicate rings
additional ring

second circle
doubling of vessels
repetition of vessels
half ring
half-annual ring
divided ring
secondary ring
secondary zone
sub-ring
intermediate ring
intermediate layer
intermediary ring
interrupted circle
ring appendage
midgrowth layer
frost ring
wound ring
moon ring (term with several meanings)
doublets
triplets

The process of doubling has also been called " duplicity ".

Attention may here be called to the use of several confusing terms in connection with growth layers in general. The designation " ring " may mean a diameter increment for an entire period of growth as seen in cross section, that is, all of the wood laid down by the cambium during such a period; or it may mean such an increment even when it does not go completely around the circumference, as in a lens. Or again, it may mean merely the outer boundary of such an increment. Often the term is used in several senses in the same article. When a ring is described as being " absent ", it may mean that there was no increment at all for the given period, the cambium having remained dormant, as may be the case at the base of the trunk in badly suppressed trees or in limbs and trunk after complete defoliation by insects; perhaps the best term for such cases is " omitted rings ". Or again, " ring absent " may mean that the cambium failed to become dormant at all, so that the wood was laid down without interruption for two or more years; in this case it is not the ring which is absent, but merely the boundary. Such cases are well known in many tropical trees, in cacti and in certain other plants.

Since double rings do exist, and since they often resemble single annual rings (see below), there arises the question of the accuracy of ring counts in determining the age of a branch or trunk. This was, of course, doubted by all who did not recognize growth rings as annuals. For those who considered multiple rings as rarities, their relation to age was of little significance; for others they assumed a much greater importance, even threatening the very foundations upon which rests the science of forestry (Fernow, 1887, 1888).

Duhamel (1758), cited above, was probably the first to give reasonably accurate evidence that ring counts do not necessarily agree with age. This followed by a half century or more the " proof " by Malpighi, Grew and Leeuwenhoek that they do agree. Winterfeld (1791) also was not convinced, for he doubted that a large number of rings in an oak proves great age in the tree. Doubts were entertained by Cotta (1806) who nevertheless considered ring counts to be the most accurate method of age determination known.

The problem of age is not yet settled. While workers in all fields—botany, forestry, archaeology—recognize the presence of

false rings, there are some who believe in the absolute accuracy of ring counts as indicators of age; others are certain that errors are bound to occur. It is, of course, not a question of the mere presence of multiple rings, but, instead, one of whether they can always be recognized as such.

A large part of the confusion on multiple growth layers arises from their variable anatomy, and this depends in part on the time of their formation (Späth, 1912). If they arise from a cambium which has been rejuvenated after complete rest during summer, the second ring shows the same anatomy as the first, and neither can be distinguished from a normal annual growth layer. Over a century ago, Unger (1847) reported five conditions in the outer boundaries of the first and second rings: that of the inner ring less sharp than that of the outer, which is the most common situation; the boundaries of both rings sharp in *Sambucus*; that of the inner sharper than that of the outer in *Robinia*; in the case of three growth layers in *Salix* and *Alnus,* the outer boundary of the inner ring sharper than those of either of the two intra-annuals; and finally, neither boundary sharp in *Corylus, Robinia, Populus* and *Salix.* And Jost (1893) found three types of outer boundaries on the inner ring—distinct, indistinct and none; the type of boundary depends on the stage of the late wood in the first ring at the time the second ring begins to be formed. Jost's last type of boundary creates what Glock (1951) has called an "invisible ring". Treviranus (1835) stated that the second ring is formed only if there is a break in the growing period; many others have agreed. If, on the other hand, rejuvenation takes place before the cambium has reached a complete rest (has merely slowed down in its activity), the boundary between the first and second growth layers will not be sharp; and the sharpness increases in proportion to the degree of slowing down. Jost (1891, 1893) alleged that the presence of double growth rings depends on the stage of development of the first ring at the time of formation of the second tip flush, and that the intermediate boundary can be sharp only if the cambium has already formed late wood in the first ring. The same idea was expressed in the same year by Strasburger (1891) and later by Priestley (1928). Hence one finds all degrees of sharpness in this boundary from that of a typical annual growth layer to an invisible one. The botanical

literature is replete with descriptions, drawings and photographs of all intervening stages (Th. Hartig, 1837a, b; Nördlinger and Poirson, 1845; Unger, 1847; Wigand, 1854; Nördlinger, 1861; Ratzeburg, 1868; Goeppert, 1868; Ratzeburg, 1871; Nördlinger, 1872, 1874; Kny, 1879; Jost, 1893; Kühns, 1910; Späth, 1912; Sorauer-Dorrance, 1914; and many others). Quite similar conditions have been found to exist after defoliation by insects or storms (Kny, 1879; Wilhelm, 1883; R. Hartig, 1892a; Petersen, 1896; Lutz, 1897; Schrenk, 1898; and many others).

The number of additional growth layers present in a multiple series is usually one, that is, the layer is usually double. Three layers in one growing season are reported by Nördlinger and Poirson (1845), Unger (1847), Rossmann (1865), Ratzeburg (1868, 1869), Fernow (1887), Antevs (1917), Gates (1924), and by Illick and Aughanbaugh (1930); these cases are nearly all in native uninjured trees in the North Temperate Zone. Three rings a year are normal for some citrus fruits in California (Reed and MacDougal, 1937; Bartholomew and Reed, 1943). A number of instances of more than three growth layers in a single season have been reported in milder climates (Richard-Martins, 1864; Ratzeburg, 1866; Warring, 1877; Wright, 1901; Chamberlain, 1921; Child, 1882, 1883; Glock and Reed, 1940; Glock, 1951).

Do multiple growth layers usually accompany multiple tip flushes? If one may judge from the statements found in the more than 50 papers seen on this subject, there is no single answer to the question: often they definitely do, more frequently they do not. The problem was recognized at a very early period, Duhamel (1758) implying that second diameter flushes are present below all second tip flushes. John Hill (1770), who put the cart before the horse, stated that each time a growth layer is formed in the wood, the branch shoots out in length. All of the early workers reported such correlation, as Bechstein (1821), Hartig and Hartig (1836), Th. Hartig (1837a, b), in oak only; this generality is probably due in part to the fact that they did not consider a structure to be a second growth ring unless it was quite prominent. Later workers became more exacting. Their disagreement may also be attributed to failure to take into account the degree of maturity of the first tip flush at the time of beginning of growth of the second tip flush. And it may further be due to differences in

the part of the tree examined; it has been shown by Kny (1879), Jost (1891), Schrenk (1898), Kühns (1910), Späth (1912) and Wight (1930) that second growth layers often extend downwards on the branch only a short distance, usually not reaching the trunk at all and becoming progressively thinner downwards.

An opposite question is in order: are second growth layers formed without the presence of second tip flushes? Apparently they are not; they seem to be found only on branches below second tip flushes.

Little or nothing seems to be known about the formation of second diameter flushes in the cases of second flowering and fruiting (Gill, 1933), nor in proliferations in cones and compound fruits.

The causes which have been held responsible for the formation of multiple growth layers parallel very closely those which have been discussed for the production of multiple tip flushes. Our knowledge of the relation of growth hormones to cambial activity is as yet too meager to have been extended far into the problem of second growth layers.

Good discussions of multiplicity in diameter growth are found in Späth (1912, 1913), Antevs (1917), Küster (1925) and Büsgen-Münch-Thomson (1929).

GROWTH IN THE TROPICS

What would the botany of today be if all early centers of botanical research and most of the later ones had been located in the tropics instead of in the Temperate Zone? The many " irregularities " of growth in the tropics would, of course, have been considered " normal ". Early botanists would have made only occasional excursions into the Temperate Zone to study the " abnormal " conditions found there, conditions which they may well have considered to be primitive because so much less complicated and more regular and uniform.

Such might very well have happened, for, as has already been shown, Theophrastus had at hand more information on semitropical and tropical plants than on those from farther north. And his work might well have been continued in Alexandria, Egypt, and spread from there to the south, east and west.

As it is, relatively little work has been done on plant growth in

the tropics. And there is much confusion because of the inability to give a clear definition to the concept, tropics. The areas generally included in the term range from perennially wet to alternating wet and dry to quite dry; from sweltering forest to scrub to grassland to desert; from sea level to perpetual ice on the high mountains. Most of the work done in these regions on tree growth has been purely descriptive of tip and diameter flushes, little or no correlation being usually attempted with total rainfall, seasons of rainfall, temperature or habitat. Therefore such excellent books as those of Gamble (1881, 1902) on the trees of India and of Record and Hess (1943) for the tropics of the New World lose much of their potential value unless the reader takes time to study the range, climatic conditions and habitat for each species—where this can be done. Nevertheless, descriptive work is quite valuable and has been accomplished with greater or less completeness in nearly all regions of the world which can be called tropical and subtropical: on the continent of Asia, in Java, Sumatra, India, Ceylon, Japan, Formosa, the Philippines and Aden; in Africa, the Libyan Desert, the Sudan, the Gold Coast, the Cameroons, Southwest Africa and the Seychelles Islands; in America, Brazil, Uruguay, Chili, Trinidad and tropical America in general; and in Australia, New Zealand and Hawaii. It is not intended to imply that there do not exist some excellent papers in which growth has been well correlated with climate and habitat; representative examples of such are those of Reiche (1897) in Chili, Simon (1914) in Java, Klebs (1926, etc.) in Java, Chowdhury (1939a, b, 1940) in India and especially of Coster (1927, 1928) in Java.

Certain changes take place gradually as one goes from the north toward the tropics. Theophrastus reported an increase in the number of growing periods from one or two in Greece to three in Crete and northern Egypt to four farther up the Nile; the length of the growing season also increases southward until it scarcely stops at all or is even continuous throughout the year; that is, the trees become evergreen. It is true that Theophrastus did not necessarily have the same species in mind, but he was able very definitely to see the tendency. Much later, and in the same region, Ascherson (1874) reported on a trip in the Libyan Desert; leaves remain on longer and longer as one goes south; one would imagine that they would reach an evergreen status near the equa-

tor.   Büsgen-Münch-Thomson (1929) stated that species which are deciduous in Europe may be evergreen in the tropics.   Timber transplanted from the north into the Malay Peninsula, according to Ridley (1901–1902), retain a tendency to form clearly-defined rings.   In quite another part of the world, Penhallow (1907) reported on gymnosperms in a line from New York to Florida.   He gives the constancy of the annual character of growth layers in the northern latitude as more than 99 per cent; the common red maple, *Acer rubrum*, which in the north quite generally forms a single ring in one year, will form at least 40 rings in less than 30 years in Florida.

The oldest known problem of tree growth in the tropics and the one which has received the greatest amount of attention is that of foliar periodicity.   The contribution of Theophrastus to this phase of the problem has already been discussed.   Then, after a lapse of many hundreds of years, botanical investigation in the tropics was revived by the explorations of Columbus, the Spanish, Portuguese, English and the French.   There is reason to believe that a good deal of useful and interesting botanical information lies hidden in archives in Spain and Portugal, which have scarcely been touched by the botanist.

The topic of foliar periodicity has so often been summarized (Simon, 1914; Coster, 1927, 1928; Schimper-Faber, 1935; Weevers, 1949; Curtis and Clark, 1950) that a review here would be superfluous.   The major topics involved are types of buds, number of tip flushes, gregarious flowering, limb-by-limb periodicity, continuous development, correlations with climate and the weather, and both external and genetic causes.

Study of growth rings in the tropics has been even more difficult than that of tip growth.   This has come about mainly because of the complexity of leaf and twig periodicity, but also in part because of the almost complete absence of coniferous species, except in the mountains.   Growth layers in conifers are generally sharply bounded, even in tropical mountains.   On the other hand, broad-leaved trees show less sharply defined boundaries at best, and are especially indefinite in tropical regions, where they constitute almost the exclusive population.

It is not known who made the first comparison between growth rings in the Temperate and Tropical Zones.   Link (1798) is said

by Bary (1884) to have reported total absence of ring boundaries in the " tropics ". However, Ursprung (1900) noted that in a later edition, Link (1824) recognized rings as being present in warm regions but with boundaries less sharp than those in temperate regions.

Rest periods in cambial activity, with consequent formation of more or less well-defined growth layers, would be expected in tropical regions of alternating wet and dry climate. Brandis (1879) demonstrated the annual character of rings in a teak plantation of known age. In the same year, however, Fernandez (1879) claimed two rings a year for a teak coppice. Sharply bounded rings have been found in abundance in eastern Java, where a dry season is followed by one of alternating wet and dry periods, by Coster (1927, 1928) who has gone most deeply into the relation between growth layers and tropical climates. Similar situations have been reported from several parts of the world, especially where the second climatic period is more or less uniformly dry. Nevertheless, rings are also rather well defined in many species in the tropical rain-forest climate of central Java (Coster, 1927, 1928), especially in those species which range also into the eastern part of the island.

Growth layers in many tropical trees have, however, been found to be multiple. In the early part of the nineteenth century an argument raged long and very warmly as to whether the gymnospermous genus *Araucaria* has growth ring boundaries at all; and gradually other tropical trees were brought into the picture. An anonymous paper (1844) reports more than 60 rings in a 34- or 35-year-old baobab tree in Senegal, and Richard-Martins (1864) described one-year-old branches of *Phytolacca dioica* three to four meters long, grown in the Montpelier Botanic Garden, which had developed up to seven rings. One may wonder about the accuracy of a report by Warring (1877) on four in *Chenopodium,* especially as the place of growth and the habitat are not mentioned. It is quite certain that Charnay (1881–1882) was inaccurate in his interpretation of the 18 rings which he found on trees that had grown in excavated ruins in Central America (or Mexico) in a known period of 18 months; these must certainly have been the common concentric intra-annual lines so common in tropical wood (see below).

More accurate are some later reports. Baldwin (1884) stated that growth rings do not give the age of a tree in Florida. In dry central Uruguay, D. Christison (1891) reported an acacia tree six and one-half years old with 20 rings, another five years old with 40, and a specimen of *Melia* 11 years old with 18 rings plus nearly 100 very distinct " quasi circles ". In Brazil, J. Huber (1898) recorded that a planted one-year-old Hevea tree formed five end-on-end tip flushes from its terminal buds at periods 40 to 50 days apart; each time there was a lengthening of the axis, unfolding of the leaves, and a maturing of the leaves; after the leaves of the first five periods had fallen off, there were three more such tip growths, making a total of eight end-on-end tip flushes in one year. The same tree made three additional such end-on-end tip flushes during the next year. Multiple tip flushes in seedlings have also been recorded by Burgsdorf (1787) and by Th. Hartig (1859).

Following 1900 the number of papers reporting on the tropics is larger, many of them being on cultivated crop trees of known age and hence no doubt quite accurate.

Because of multiplicity, Coster (1927, 1928) estimated that ring counts in the tropics, when used in age determinations, represent an error ranging from very little for some species to 20 or 30 per cent for others. Under such conditions increment borings are of course of no value for age counts (Hutchinson, 1927).

The extreme opposite relation of growth layers to climate is reported by Holtermann (1902) for extremely dry Aden, where several years may pass without any rain; trees said by the natives to be 30 years old show only five or six rings, one ring apparently for each rain.

Even when growth layers are present in abundance and where their boundaries are relatively sharp, there is often little evidence that they are annual. They seem to vary with the vagaries of the weather, and the necessary careful work required in keeping records on individual marked twigs does not seem to have been done.

Factors and causes which have been assigned to cambial activity in the tropics do not differ materially from those assigned to growth layer formation in the Temperate Zone. The joint operation of several factors must, however, be far more complex. Coster

(1927, 1928) reported that growth rings are often correlated with tip flushes, as would indeed be expected from our present knowledge of the relation of growth hormones to cambial activity in the Temperate Zone.

In the tropical rain forest, certain species which are endemic there show continuous diameter growth. This means that the cambium continues its activity without a rest period at any time and that the wood may be a number of years old without showing any signs of ring boundaries. Continuous growth has been abundantly observed.

The anatomy of the growth layers of many tropical trees is far more complex than that of trees of the cooler zones. Such complexity can be only partially associated with climatic and weather conditions; it is largely inherent. A few examples, selected to show only the variations in the types of boundaries, are indicative of the anatomical complexities found in the growth layers. In " Timbers of the New World " by Record and Hess (1943), more tropical families are included than families of the Temperate Zone. The boundaries of the growth layers, when present, can be recognized in various ways, which we have summarized from a study of each individual description of the many genera in some 123 families, as follows:

  I. Tracheids in conifers.—No information given, hence it is assumed that determinations can be made in the manner usual for this group.

  II. Vessels.
    1. Ring-porous condition present to a greater or lesser degree; greater or lesser zonation in the early wood.
    2. Difference in density of the pores (much as in the preceding).
    3. Difference in size of the pores.

  III. Wood fibers in dicotyledonous woods.
    1. Difference in radial dimension is sometimes limited to a narrow zone of late wood.
    2. Difference in wall thickness.
    3. Local difference in " density " (overlaps the two preceding).
    4. Prominent alternating bands of early and late wood.

IV. Parenchyma in the xylem.
  1. Presence of terminal parenchyma or of a narrow band of parenchyma.
  2. Wider spacing and more orderly arrangement of the parenchyma.   Periodic wider spacing of parenchyma bands.   Difference in the spacing of parenchyma layers.
  3. Presence of narrow bands of tissue deficient in parenchyma.
V. Late wood darker in color than early wood.

This summary of criteria for boundaries agrees rather well with a similar one which we have compiled from a study of 81 species in 61 genera in 29 families of Sumatra woods (Cockrell 1934):

  I. Vessels: number, size, absence of, the more porous zone at the boundary, vessels in a zone of fibers, tangential band of vessels.
  II. Fibers: change in density, radial flattening, thickness of wall.
  III. Parenchyma: presence of terminal parenchyma, radial flattening of parenchyma cells, fewer parenchyma cells in outer part of the ring, greater abundance of metatracheal parenchyma at the boundary.
  IV. Rays: flaring, distortion, or bending at the boundary.

Such a host of variations at the boundary alone can make the anatomy of tropical growth layers very complex, indeed.   In many instances above, two or even several of these criteria may occur together at the boundaries of a single species.   No effort was made by these authors to determine whether the growth layers are annual.

The reasons assigned for multiplicity of growth in the tropics run the usual gamut of drought, defoliation, food, heredity, etc. It would seem that the tropics represent a virtually unexplored field for work with growth hormones.

A significant aspect of the problem of tree growth in the tropics involves the reaction of native Temperate Zone trees when transplanted into a tropical region.   Holtermann (1902) reported that such transplants to the tropics retain their periodicity for some time.   Pfeffer (1903) stated that trees transplanted to different climates tend gradually to adjust themselves.   According to Ding-

ler (1911), English oaks transplanted to the highlands of Ceylon show an irregular leaf and tip growth periodicity. Coster (1927, 1928) believes that conifers introduced from the Temperate Zone into Java retain their leaf periodicity; such transplants had, however, been made into the mountains. Many dicotyledonous trees, on the other hand, soon alter their leaf periodicity to one in which different limbs on the same tree lose their leaves at different times. On the whole, he finds in such transplanted trees a rather close relation between leaf periodicity and cambial activity, the latter not extending very far down the limb or very far into the trunk. While most introduced trees continue to form rings, they are often not annual and the sharpness of their boundaries is quite variable; there are also many intra-annual irregularities.

Reiche (1897) reported on transplants from the Northern to the Southern Hemisphere. He found that in general fruit trees transplanted from central Europe to subtropical Chili gradually become adapted to the seasonal changes in Chili, the peach becoming almost evergreen. The more recent literature on transplants into Australia, New Zealand and South Africa is along the same lines as the above.

A transplant from the tropics into the cooler zone was studied by Fischer (1905). A japanese larch, which in its native land presumably shows abundant multiplicity, retained this tendency in Germany, forming from one to six tip as well as one to six diameter flushes a year between the years 1898 and 1905.

Before arriving at conclusions on growth in the tropics, several recent papers merit brief mention in order to show the trend of research. Chowdhury (1939a, b) refers to continuous cambial activity in some species in India, and discontinuous growth in others. Walter (1940) finds a rather close correlation between precipitation and ring thickness in southwest Africa; the curve indicates a short weather cycle of 9.53 years and a longer one of 20.25 years. He extends the curve into the future and makes a tentative weather forecast from it. I. W. Bailey (1944) finds that ring boundaries vary from good to absent in the tropical family Winteraceae. He concludes that there are two distinct types of zonation phenomena in wood: (a) obligate rings, as those in many trees of the Northern Hemisphere; and (b) facultative rings, like those in many plants of tropical and subtropical regions as well as plants of the Southern Hemisphere, in which the formation of

boundaries is entirely dependent upon the environment. On the Gold Coast of Africa, Hummel (1946) finds growth layer boundaries not only often present but in many cases of an annual character, so that ring counts may be expected to give a fairly reliable estimate of age in some species. In other species the cambium is active twice a year, and in certain others cambial activity is variable from year to year. Often many intraseasonal irregularities, such as bands of varying sharpness, are present, and cambial activity often follows the flushing of leaves. Jane (1934) and Chowdhury (1947, 1953) find initial parenchyma to constitute a very common type of boundary in the tropical trees of India; it had previously been supposed that this tangential layer of parenchyma is always formed at the close of the growing season, in which case it is of course terminal parenchyma. Chowdhury (1939a) had already called attention to the incorrectness of our usual interpretation in the genus *Terminalia*. Humphries (1947), working with the cacao tree in Trinidad, shows that starch is used up as the cambium becomes active; there is no real rest period of the cambium, although there are several cycles of growth each year.

Certain conclusions may be derived from the work on the growth of trees in the tropics. Multiplicity is rampant in both tip and diameter growth. At least in most species, none of the usual methods of determining age can be relied upon. There is usually little reliable correlation between growth and climate, growth and weather, or between tip growth and diameter growth. It is probable that the tropics will prove to contain the most promising geographic regions for solving some of the complicated problems of both tip and diameter growth in trees and shrubs.

GROWTH OF ROOTS

The underground parts of plants have never received the attention which they deserve. Their unpopularity is of course due to the difficulty of studying them in their native environment. This applies not only to the roots of trees, but to other roots as well, and to rhizomes, bulbs and corms.

Because their environment, the soil, is much more uniform than the aerial environment of the stem, the growth responses of roots are in many respects comparable with those of stems in a tropical rain forest. This is true of both length and diameter growth.

It is difficult to find a botanical subject which was not touched upon by Theophrastus. In his " Enquiry into Plants " (Hort, 1916) we find the statement that no root goes down farther than the sun reaches, since it is heat which induces growth. And in the " Causes of Plants " (Dengler, 1927) Theophrastus tells us that he did not completely agree with those who said that roots grow in the fall and winter, while trunks and branches grow in spring and summer.

Indeed, the question of periodicity in length growth has been one of the major research problems on the roots of forest trees. The problem interested the French botanist and forester Duhamel (1758, 1760) who found growth to occur during the winter. There is, however, no definite period of length growth for all trees, although much of it does actually take place in the autumn and even through the winter, often in several growth spurts. The result is, of course, multiplicity in length growth, although the boundaries between the successive tip flushes are poorly defined or not at all. Roots are much more likely to die back than are stems, which adds to the complexity of studying their tip flushes. When root growth is described, especially as occurring in the winter, it may mean length growth of the tap root or of already existing lateral roots, or the formation of new lateral roots, or both tip and diameter growth. The bud-root theory of root growth has been discussed earlier in this paper.

Relatively little is known about diameter growth in roots. Multiplicity is quite common, as are also many types of partial rings and indistinct boundaries.

A closer study of roots should also help solve some of the fundamental problems of tree growth. Many of these problems are summarized by Bischoff (1836), Mohl (1862), Engler (1903), Hilf (1927), Lodewick (1928), Büsgen-Münch-Thomson (1929), Mac-Dougal (1938), J. F. Reed (1939) and Kramer (1949).

It is of interest that Grew (1682) first used the word " cambium " in a study of the anatomy of the root.

CAUSES OF GROWTH

The causes of growth can not be discussed without a definition of terms. To the layman, resumption of growth in spring is caused by the rise in temperature; to the botanist, the problem of tem-

perature has receded from a cause to a mere modifying factor. This has been the fate of nearly all " causes ". At the present time, growth hormones are considered causal, but it is very probable that they, too, will become merely important factors when we possess more fundamental knowledge about them.

It is not our intent to review either the " factors " or the " causes " of growth, for these may be found in many modern textbooks of plant physiology and plant ecology, as well as in the histories of botany. An excellent summary is contained in Büsgen-Münch-Thomson (1929). We desire, instead, to call to the attention of the reader several forgotten chapters in the history of our knowledge of plant growth.

We return once more to Theophrastus' " Enquiry into Plants ". In the translation into German by Sprengel (1822) we find this statement: " If one permits the buds to remain on the trees, the latter grow rapidly in length; if they are removed early, the trees become more compact, like the grapevine ". According to Ernst Meyer (1832), Duhamel reported at the middle of the eighteenth century that length growth of the horse chestnut is stopped by cutting off the tip at an early stage while still in the herbaceous condition. And Burgsdorf (1783) said that leaves are most important in that they precede all development in the mature plant; each leaf furnishes the materials needed for the growth of the node below it.

Credit for having first suggested that growth may be due to a stimulating substance (hormone), not merely to food materials, is given to Sachs for the year 1880 by Möbius (1937) and to Charles Darwin for the year 1881 by Crocker (1948). Mer (1892) believed that the differences between spring and summer wood are to be explained by the plastic materials (as opposed to foods) which become available to the cambium. Coster (1928) expressed the opinion that some substance or stimulus originating in the developing leaves and passing downwards through the phloem is responsible for initiating the growth of the cambium; this stimulus, which is not a reserve or a new food, he believed more likely to be a hormone. However, as is often the case, the practical farmer anticipated the scientist. There was in use in France a horticultural practice which involved external application of some type of " growth substance ". In the Oelhafen translation of

Duhamel into German (1765), we find the following: " Some writers recommend that the end of cuttings be dipped in a certain mastic salve, whose preparation is described with much circumstance; they claim that it results in the rooting of the cuttings. I have tried this suggestion, but believe that the formation of the swelling which precedes the new roots was somewhat delayed, since the swelling, instead of being formed at the end of the cutting, was formed above the putty [used instead of grafting wax]. Therefore, I concluded that the method at least did no good, and may be damaging ". Information on the contents and the method of preparation of this concoction would be of considerable historic and scientific interest; since its use was apparently a somewhat common practice, at least in France, it should be found in the French horticultural literature of the day.

A stimulus, although not in the sense of a hormone, is referred to by Hundeshagen (1829); he considered the possibility that one cause of multiplicity in tip flushes may be the stimulating influence of the increase in sap flow at that time of year.

One very sugary morsel of history has apparently been completely missed by the reviewers of botanical literature. In 1868 the German plant physiologist Sachs (1868) postulated a theory that bark pressure is the cause of the difference between spring and summer wood. His statement is as follows: " The cause of this difference has not been heretofore known, but I would guess that it is simply dependent on changes in the pressure exerted on the cambium and wood by the surrounding bark; this pressure is less in the spring but becomes increasingly greater toward the autumn; I do not have direct measurements, but arrive at this conclusion from the fact that the longitudinal splits in the bark made in February and March become broader, as seen clearly in *Quercus, Acer, Populus, Juglans,* etc.; I will not discuss the causes of this increase in pressure, but nevertheless, the bark, whose longitudinal splits have become widened during the winter, exerts a diminished pressure on the cambium in the spring, so that the wood cells are then more easily enabled to expand radially; the pressure on the cambium must then constantly increase because of the thickening of the woody cylinder on one side and the drying out of the bark during the summer on the other side, and accordingly decreases the radial growth of the young autumn wood cells.

Further investigations, which I am planning, will show whether my theory is correct". (In Sachs' day it was thought that the late wood is formed in autumn). Later, Vries (1872*a*, *b*, 1875, 1876) presented what seemed to be incontrovertible proof of Sachs' theory, which the latter author repeated in later editions of his physiology text. Some years later, however, measurements made by Krabbe (1882, 1884) showed that, although bark pressure does indeed exist all through the year, the difference in the measured amount of pressure during the different seasons is far too small to account for the differences between spring and summer wood.

This much is a well-known part of the history of botany. But Sachs, "author" of the bark pressure theory and the historian of botany, had the misfortune altogether to miss the fact that his theory had been brought forward in considerable detail just 85 years before he made his own suggestion!

We have already met Burgsdorf in several connections in this paper and shall meet him again. Although his name does not appear anywhere in Sachs' "History of Botany, 1530–1860" (translated by Garnsey and Balfour, 1906), to Burgsdorf seems to go the credit for having first proposed bark pressure as the cause of tree rings. In reading his statement of his theory, it should be remembered that the cambium was not considered to be a tissue in his day and the splint, a term applied to the inner layer of "bark" was believed to become converted into true wood. Translated, his statement is as follows (Burgsdorf, 1783, pp. 232–233) :

The growth of this young splint continued until the sap becomes concentrated in the late autumn, the twig having long before completed its growth in length.

Now, the more the splint hardens on the outer face of the true wood, and the smaller the amount of sap which passes through it, the more does this coat [splint], together with the bark, pull itself together, since the causes for further expansion have now been removed; rather do these causes now result in a coagulation of the small amount of sap present.

So there comes about a drawing together and a pressure from the outside, from the circumference toward the center. The splint of the preceding year becomes compressed evenly, and it, in its turn, presses evenly on the pith.

All of the tissues inside of the new splint therefore become more dense, being surrounded by the young hardening splint; and the outermost part of these inner tissues now becomes true wood which differs from the splint only in its greater density and dryness. Because the pressure of the splint

on the wood operates most effectively on the outer surface of the wood, there is produced at that surface the much denser layer [late wood] which represents the identifying characteristic of the ring. . . .

In his second volume, Burgsdorf (1787, pp. 94–95) used his pressure theory to explain the conversion of white wood (sapwood) into ripe wood (heartwood); and again (p. 100) we find the statement that as the inner bark dries it is constantly compressed inwardly.

Although Burgsdorf did no experimental work, his statement of the pressure theory as applied to the formation of growth layers is as clear as is that of Sachs—who also had done no experimental work on the problem.—The light of Burgsdorf should shine much more brightly on the pages of botanical history. Sachs can be forgiven in part, for all of Burgsdorf's statements used in the present paper are well hidden, with no suggestion of their presence in the titles of his books, nor in his chapter headings; and since there are no indexes, they can be discovered only by stumbling upon them.

Willdenow (1792) expressed much the same idea as did Burgsdorf, only much less clearly: " A new circle of vessels [all elongated cells in the wood] is formed annually in the stem around the older circle, which crowds the inner circle closer together . . . in the course of time, however, several circles of vessels have become formed, which crowd the innermost circle into greater compactness . . .". At another location he considered bark pressure to be the cause of thin rings: " If the bark is too firm, then there are formed annually only thin wood rings ", both in trees and in shrubs. A few years later Cotta (1806) held that the change from splint to wood, the wood being denser and harder, could in no wise be the result of a greater pressure from the outer parts, for in that case transition could be only gradual and thus could not result in the sharp boundary between splint and wood (i.e., between two adjacent rings). Theodor Hartig (1860) maintained that there is no bark pressure at all in trees during the summer. Almost simultaneously with Sachs, Kraus (1867) showed that an enlarging stem does exhibit bark tension in the summer, but he did not obtain quantitative results of value. Nördlinger (1870) showed the presence of bark pressure during the summer in pine, larch, birch and oak. The same author (1872) also showed that rings become thicker after ripping of the bark and releasing of the

pressure on the wood. Again two years later, he (1874) disagreed with Vries (1872). N. J. C. Müller (1876) considered bark pressure to be the cause of ring formation. A few years later, Nördlinger (1880) modified his view somewhat; although he considered bark pressure not to be the cause of growth rings under normal conditions, there are many cases, he said, of wavy outlines in trees, shrubs and vines, as seen in cross section, which are best explained by supposing them to be due to irregularities in bark pressure. Penhallow (1885) did not believe bark pressure always to be applicable. Janowitsch (1895) also dealt with bark pressure. Schwarz (1899) discussed the power of the plant to react to bark pressure, and Sorauer-Dorrance (1914) followed Vries and discounted Krabbe.

Thus we find that, preceding Sachs' first statement of his idea, the same thought had been mulled over by Burgsdorf, Willdenow, Cotta, Hartig and Kraus.

INTERNAL MARKERS

The problem of dating an individual growth layer in a tree with absolute certainty is a difficult one. A simple counting of rings is, of course, quite uncertain, since there is always a possibility that multiple rings may be present, or even that the cambium may have failed to lay down a growth layer at all during a given year. In anatomical work it is often necessary to know the date of a specific ring, or it may be desirable to know whether during a given year one or more or perhaps no ring had been laid down by the cambium.

Among the several methods by which such determinations may be made with absolute certainty is that which may be called " internal markers ". In its simpler form the method is very old and consists of finding some mark which Nature herself has placed in the wood of a tree at a known time. The literature on this subject is extremely voluminous, including, as it does, identifiable rings resulting from defoliation, drought, fire, lightning and unfavorable weather conditions. Dating back to the severe winter of 1708–09 will be discussed in the next section. Although Theophrastus did not know that the date of growing together could be determined by counting the superimposed growth rings, he nevertheless made this interesting comment (Sprengel, 1822) : " For it

often happens that one part of a tree, which has grown together with another part, becomes enclosed by the latter ". Waterhouse (1811) said: " Who knows, but we may hence form a probable conjecture of the age of those surprising antiquities [Indian mounds], discovered in this new world on the banks of the Ohio and Muskingum? " Agardh (1829, 1830), living in an age when the world was still believed to be only 6000 years old, spoke of the possibility of using trees to tell us the age of coal measures, limestone strata, etc. Similarly, Candolle (1827, 1831, 1833b) suggested the use of tree rings for determining the age of monuments, of talus slides, of changes in dunes and river beds, of the origin of volcanic and coral islands, and of the " last revolutions of the globe " (cataclysms).

Hough (1882) believed from a study of sections of tree trunks in museums that it is possible to date accurately insect injuries of a century or more back by certain characteristic thin rings. Baldwin (1884) reported that Prof. Jeffries Wyman proposed to reach a conclusion of the approximate age of some Indian mounds in Florida by counting the rings of trees growing upon them; this was probably not done, for Baldwin had called his attention to the inaccuracies inherent in the many multiple rings present in the trees of Florida. Robert Hartig (1892b) used hail injury of a known date to determine whether annual diameter increments had reached the base of the trunk in closed pine stands; he found five growth layers to be absent at the base. Similarly, Rubner (1910) used natural frost injury to date the rings formed above and below a constriction placed on the trunk. I. W. Bailey (in Swaine, Craighead, and Bailey, 1924; Bailey, 1925a) employs natural frost rings in determining the dates of certain growth layers. In the first paper just mentioned (1924), as well as in a later one (Bailey, 1925b), he relied on abnormal growth rings caused by insect defoliation as a criterion of age. Glock and Studhalter (1948) discuss natural frost rings as a tool in dating, and Glock (1951) elaborates further on the idea. In fact, the entire method of cross-dating by use of narrow rings is a part of this phase of the problem.

In an excellent piece of work, Enos Mills (1904, 1908, 1909a, b, 1914) dissected a large yellow pine, *Pinus ponderosa,* in the Rocky Mountains and reconstructed its life history from internal

evidence. His conclusions were based on the belief that each of the 1047 growth rings represented the diameter increment of a single year. At 135 years of age, some limbs broken off of a falling neighbor were embedded in the old pine, to be covered over in 12 years. A year or two later, ants and borers became active, their activity soon to be reduced by birds (woodpeckers, etc.). It was struck by lightning at the end of the summer of 1301. Checking and shattering between 1811 and 1812 are interpreted as having been caused by an earthquake shock. Also between 1811 and 1812, a five-pound stone bounding down the mountain side struck the tree so violently that it became embedded; it ultimately became healed over and remained hidden until Mills found it. This is only a single example, a rather early one, of trees for which life histories have been read from internal evidence.

Of greater significance, perhaps, and certainly of greater human interest, are internal markers of one kind or another which man himself has deliberately placed into the trunk or branch of a tree. For the first such case on record we must go once more to Theophrastus (Sprengel, 1822; Hort, 1916). We find this statement: ". . . and if one forces a stone or some similar object into a tree, it becomes hidden, since the new growth surrounds it, as was the case with the wild olive tree which stood in the market place at Megara ". While the purpose of forcing the stone into the tree is not stated, the conclusion that new wood is deposited over the old is inevitable.

The indefatigable Duhamel used internal markers in many of his experiments in an effort to determine how the new bark and new wood are formed. In one set of experiments (Duhamel, 1751) he described the placing of small strips of tin foil at definite depths in the cut bark or cut wood, tying the bark and wood back into place, treating with an antiseptic, and examining again at the end of the growing season. In other experiments, fine silver wires were forced through the bark and wood at approximately known depths. He was able to draw important and mostly correct conclusions about the manner of growth of both bark and wood. The experiments are again described in his classical " Physique des Arbres " (Duhamel, 1758) and in the Oelhafen translation into German (1764, 1765).

The carving of dates, initials and other markings through the

bark of a trunk is another example of this method. Burgsdorf (1787) used an axe mark of a known date, namely, August, 1767, on an oak tree at a boundary line as proof that only one ring is formed each year; in November, 1785, the blaze was covered by 18 growth rings. Goeppert (1868–1870) cited many cases, beginning with Bartolinus in 1654, in which inscriptions through the bark of trees as well as monuments (the nature of the latter not explained) were used in proving that growth layers are annual, for in every case the number of layers corresponds with the number of years which had elapsed from the date of the inscription or monument. The same method had already been used by Candolle (1827, 1828, 1831, 1839, 1839–1840), described by Bischoff (1836), Jussieu (1843), Nolte (1846), Lindley (1848), Jaschke (1859) and Ratzeburg (1866), and long ago suggested by Schober (1753).

Numerous legal cases involving property rights have been settled in court from the blazes left by surveyors on the trunks of trees along boundary lines (P. C. Smith, 1883; Child, 1883; Hotchkiss, 1894; Fernow, 1888, 1897). In nearly all cases the court accepted the dictum that tree rings are annual; however, at least one case is on record (Child, 1883) in which the court ruled that growth layers are not infallible indicators of age. A case was recently brought to court in Alsace in which tree rings were used as evidence of ownership (Senn, 1933). Tree rings were used also by Tharp (Sellards, Tharp, and Hill, 1923) in a boundary dispute between the States of Texas and Oklahoma, and by Cowles (1915) in an extensive Federal lawsuit in Arkansas involving riparian boundaries.

In interpreting the life history of the old yellow pine mentioned above, Mills (1909, 1914) interpreted several situations as internal markers placed by man. In 1486 two flint arrow heads became embedded in the wood, suggesting a bear hunt or an Indian battle. A basal fire scar in 1840 may have had its origin from a camp fire of the early Spaniards. An axe mark of 1859 was probably a trail blaze. A similar fire scar in 1859 probably originated from a prospector's camp fire. In 1881 several rifle bullets became embedded around and just beneath a blaze; Mills suggests target practice as a possible explanation.

In experiments on double rings after artificial defoliation, Wil-

the title of Father of Cross-dating. It is our judgment that this man, who was so completely ignored by the historian Sachs, deserves a large place in the history of botany.

In 1827 Twining (1833) rediscovered the very essence of cross-dating. It is worth while to quote his entire brief article because it is so full of pregnant ideas:

I take this opportunity to mention a fact, which I once observed, and which may, perhaps, prove interesting to the readers of your Journal and lovers of natural science. In the year 1827, a large lot of hemlock timber was cut from the north eastern slope of East Rock, near New Haven, for the purpose of forming a foundation for the wharf which bounds the basin of the Farmington Canal on the East. While inspecting and measuring that timber, at the time of its delivery, I took particular notice of the successive layers, each of which constitutes a year's growth of the tree; and which, in that kind of wood, are very distinct. These layers were of various breadth, indicating a growth five or six times as full in some years as in others, preceding or following. Thus, every tree had preserved a record of the seasons, for the whole period of its growth, whether thirty years or two hundred,—and what is worthy of observation, *every tree told the same story*. Thus, if you began at the outer layer of two trees, one young and the other old, and counted back twenty years, if the young tree indicated, by a full layer, a growing season for that kind of timber, the other tree indicated the same.

My next observation was, that the growing seasons *clustered together*, and also the meagre seasons came in companies. Thus, it was rare to find a meagre season immediately preceding or following a season of full growth,—but, if you commenced in a cluster of thin and meagre layers, and proceeded on, it gradually enlarged and swelled to the maximum, after which a decrease began and went on, until it terminated in a minimum.

A third observation was, that there appeared nothing like *periodicity* in the return of the full years or the meagre, but the clusters alternated at irregular intervals; neither could there be observed, in comparing the clusters, any law by which the number of years was regulated.

I had then before me, therefore, two or three hundred *meteorological tables,* all of them as unerring as nature; and by selecting one tree from the oldest, and sawing out a thin section from its trunk, I might have preserved one of the number to be referred to afterwards. It might have been smoothed on one side by the plane, so as to exhibit its record, to the eye, with all the distinctness and neatness of a drawing. On the opposite side, might have been minuted in indelible writing, the locality of the tree, the kind of timber, the year and month when cut, the soil where it grew, the side and point which faced the north, and every other circumstance which can possibly be supposed ever to have the most remote relation to the value of the table in hand. The lover of science will not be backward to incur such trouble, for he knows how often, in the progress of human knowledge, an observation or an experiment has lost its value by the disregard of some circumstance con-

nected with it, which, at the time, was not thought worthy of notice. Lastly, there might be attached to the same section, a written meteorological table compiled from the observations of some scientific person, if such observations had been made in the vicinity. This being done, why, in the eye of science, might not this *natural, unerring, graphical* record of seasons past, deserve as careful preservation as a curious mineral or a new form of crystals?

If you should think fit to make such a suggestion, it might lead, in fact, to the preservation of sections from aged trees in different parts of the country, and a comparison of their lines of growth with the history of the weather as far back as our knowledge extends. If the observations just related, with respect to a particular lot of timber should be found to hold true of trees, in general, drawings of these sections, on a reduced scale, would soon find their way to the pages of scientific journals. It would be interesting, then, to make comparisons of one with another,—to compare the sections of one kind of tree with that of another kind from the same locality, —or to compare sections of the same kind of tree from different parts of the country. Such a comparison would elicit a mass of facts, both with respect to the progress of the seasons, and their relation to the growth of timber, and might prove, hereafter, the means of carrying back our knowledge of the seasons, through a period coeval with the age of the oldest forest trees, and in regions of the country where scientific observation has never yet penetrated, nor a civilized population dwelt.

Here, indeed, we have not only cross-dating with a vengeance, but a prophetic insight into the future.

The story of the cross-dating done by Kuechler (often misspelled Keuchler) on oaks at Fredericksburg, Texas, in 1859 has been told several times (Glock, 1941). Some recent papers bring our knowledge of the man and his work up-to-date. Lowry (1934) studied some oaks cut in 1934, also at Fredericksburg. For the years in which his rings overlap those of Kuechler, there is some similarity between the weather data inferred by the two men. But Kuechler (1859) obtained far too many wet years, a fact which has not hitherto been explained. A comparison between the climates of Texas and Germany may furnish a clue to an explanation. The Fredericksburg area in Texas lies so much further south than does any part of Germany, in which country Kuechler obtained his training in forestry, that the Texas growing season is no doubt much longer, and probably the rings correspondingly thicker. If this assumption is correct, Kuechler must have been accustomed in Germany to oak rings which average much less in thickness than do those in Texas, and when he saw the thicker Texas rings, he assumed them to be due to wetter

years. Hence he would interpret his data as indicating a dispro-
portionately large number of very wet seasons.

Campbell (1949) succeeded in finding the original article of
Kuechler's in the archives of the University of Texas; he calls
attention to certain errors promulgated by later commentators.
He also adds a good deal of information on Kuechler's life and
public activities.

In the same year that Kuechler wrote his article in a newspaper
in Texas, Vonhausen (1859) published a somewhat similar article
in a professional journal in Europe. Based upon measurements
of ring thicknesses in a half dozen species of trees, he found the
ring of 1858 to be thin because the preceding late summer, winter
and spring had been very dry. In every case where the same tree
was used, there was less diameter growth in 1858 than there had
been in 1857. He adds that the narrow ring will be recognized
in the trunk many years later.

In commenting on Vonhausen's paper, Nördlinger (1874, foot-
note page 166) stated that " It would seem to be desirable, in
consideration of these [external] influences, to study the correla-
tion of all narrow rings with all dry winters of the past ".

The suggestions of Twining and of Vonhausen seem to have
been almost completely forgotten. Similar suggestions made in-
dependently by Pokorny (1865–66) have recently been resur-
rected. This writer states that since climate is one of the most
important factors in determining diameter growth, it follows that
the characteristics of the weather of each year must be distinctly
reflected in the structure of the wood ring. If this is true, the
rings would become true meteorological yearbooks which, because
of the great age of many trees, would date back not only for cen-
turies but for millenia. He proposes a comparative study of the
annual rings of the same given year in different trees, and he
himself did just enough experimental work to show the feasibility
of the method. A year later Pokorny (1867) again spoke of tree
rings as meteorological yearbooks, going back hundreds and even
thousands of years.

L. H. Bailey (1885) echoed the statement of Twining when he
wrote that by their thicknesses tree rings are " meteorological
records of the years ". Similarly Baldwin (1884) stated that a
tree represents a true record of the weather, in so far as drought
and rainfall are concerned.

In a later paper Pokorny (1869) gave more specific directions for the study of cross-dating although, of course, he did not use this term. And he recommended the study of as many rings as possible with the microscope. He concluded that if these ideas are applied, trees may indeed give us the hope of obtaining information on the weather of individual years several thousand years ago. He was well aware of the disturbing influence of such factors as exposure, defoliation and the course of nutrition. Nördlinger (1872, 1874) was much less charitable toward Pokorny than he was toward Vonhausen. In fact, the objections of this well-known botanist were so strenuous that one wonders whether he did not succeed in nipping the newly proposed science of cross-dating in the bud.

Elias Lewis (1873) made the interesting comment that it had long been customary to make estimates of the ages of many standing trees from the number of rings on another tree in which rings could be counted. Ratzeburg (1866) compared the ring of a certain year, the result of caterpillar injury, in different trees, thus dating these rings absolutely. R. Hartig (1897) also used the exact principle of cross-dating in determining the age of trees killed by smoke and fumes, only that he compared two different levels of the same trunk instead of comparing two different trees. Actual ring counts at the base often proved to be impossible because of the frequent omission of rings at that level. First he selected characteristically thick and thin rings in the upper part of the bole, where he assumed all rings to be present. The number of rings formed between these characteristic rings was accurately counted. Then, at DBH on the lower bole, he located the same characteristic thick and thin rings, and interpolated the number of intervening rings from above. This gave him a close approximation of the age of the tree at its base. Andrews and Gill (1939) called attention to the fact that this is almost exactly the method used by the dendrochronologists.

Schwarz (1899) made a large number of comparisons of ring thicknesses in different pine trees for the same year, but did not seem to look upon the problem as one of cross-dating.

The astronomer Kapteyn (1914) brought out a long unpublished paper on cross-dating work on oaks in Holland and Germany, done in the year 1880. One of his conclusions is that fluctuations in ring thicknesses are due largely to subsoil moisture,

especially from spring and summer rains. Kapteyn compared the ring thicknesses from tree to tree, and therefore succeeded in doing true work in cross-dating.

Lakari (1915) in Finland determined which years between 1757 and 1900 had been good seed years in pine. A good seed year covers a large geographical area, and following such a year a large number of trees should have the same age, since they started together; ring counts showed this to be true. A similar situation exists in an area of lodgepole pine coming in after a fire, and in certain desert trees which are able to become established only after several successive years of heavy rainfall, which in the desert is a rare occurrence. A comparison of ages in these cases by ring counts is, of course, cross-dating.

This account brings the history of cross-dating up to the work of A. E. Douglas in the American Southwest, work which began about 1904. It shows that the idea has occurred independently to several men in different countries and over a period of many years. It remained for Douglas, however, to use them extensively and to apply them widely to astronomy and to archaeology.

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II. Growth Rings and Climate

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". . . to the naturalist the virgin forests of Borneo are still a wonderland full of strange questions and half-suspected discoveries."   —H. G. Wells.

CONTENTS

INTRODUCTION

Since the previous review was prepared (Glock, 1941), growth-ring studies have developed apparently along several trends: *a*) gathering of large collections of samples which cut across hundreds of miles of diverse topography, climate and soil in order to detect possible general fluctuations of climate; *b*) lessening reliance on long-time dating; *c*) lessening emphasis on growth layers as exact rain gauges; and *d*) increasing emphasis on the study of growth layers through botanical disciplines.

It is not the intention of the writer to review all articles pertaining directly to the subject because in 30 years his bibliography has grown to thousands of entries, and even the last 12 years have added more than can conveniently be incorporated here. His purpose, rather, is to trace major developments. An excellent though brief summary and discussion of current work in growth rings have been given by Dobbs (1951). In addition, criticism of specific points has been made by Glock (1942*a, b*) and by Sampson and Glock (1942).

Sincere gratitude is due the Smithsonian Institution and Macalester College for the financial support which made the review possible. Also, I am deeply indebted to many friends who, knowing of my interest in growth layers, were constantly on the watch for publications and information pertinent to my interests. For many hours of editorial assistance I am extremely grateful to Waldo S. Glock, Jr.

Zeuner (1950*b*) wrote: "The twentieth century is characterized by an expansion of prehistoric research . . .". To this expansion the study of growth layers, or tree rings, has contributed a share not only from the human and chronologic but also from the climatic standpoint. Both have exhibited extreme claims and conservative cautions; the truth very probably lies between the two.

The mathematical and dynamic approach to the study of tree growth could conceivably be the logical one (Haskell, 1940) because organisms are integrations of a pervading environment, physically and chemically, and because "the second law of thermodynamics implies universally increasing complexity" among plants and animals. At least one writer maintains that "his interest in dendrochronology lies largely in its possibilities as a branch of physical science" (Schulman, 1945*a*). Perhaps this non-biological

approach to biological problems was of concern to Davis in 1889 when, in discussing pine trees, he asked: "Why not [speak] of other vegetable growths, with straight vertical axes, from which lateral arms spread out with some regularity, bearing long, slender spicules on their minuter divisions?" (Davis, 1909).

Chronology of past events may not be of vital importance to the world today, but it is none the less a fascinating subject. Even the life history of a single pine as read by Mills in 1909 carried an interest not to be evaded. He completely dissected the tree— trunk, limbs and roots—and counted 1047 rings of growth at the base. It probably sprouted in 856 A.D. Then Mills chronicled an eventful life: at year 20 snow bent the tree; at year 135 it was stabbed by the dead limbs of another tree which fell against it; lightning struck it in 1301; two large limbs were lost in 1348; in 1486 two arrow heads were shot into the tree; in 1540 it felt steel and fire; in 1762, in 1804 and in 1805 climatic stress assailed the tree; in 1859 an ax left its mark; and in 1881 several rifle bullets penetrated the wood.

Dating the Indian Pueblos of the Southwest has constituted a romantic episode in the study of American prehistory. Such dating assumes positive identification of the annual increment of growth and relies upon a so-called master chart which represents an amalgamation of tree-ring sequences of varying length locked together over the centuries, some intervals built on many sequences, others on few. Even granting the accuracy of the chart and its wide areal applicability, and disregarding botanical and ecological questions, we encounter claims that seem unnecessarily extreme. For instance, dating has been called nearly miraculous (Davis, 1931); "one of the most important developments of modern science" (Gilpin, 1941); magic, a miracle (Abbott, 1946); a problem solved (King, 1951). Hawley (1939) stated that at first tree-ring analysis sought help from other sciences but that now it is itself a science and, "year by year, offers new application of its adaptable technique to problems in the very sciences which originally set it upon its now steady feet".

In contrast Gladwin (1943) had difficulty in reconciling certain tree-ring dates with the archaeological evidence. His appraisal of the dating situation had perhaps raised a needed caution signal. The time subject in the synthesis of a culture, he said, must "be

regarded as an intangible " one " in spite of the tree-ring dating ".
As regards the assignment and expression of dates when complete
specimens were lacking, Gladwin said: " all that can be said for this
is that it is a misguided attempt to endow tree-ring dating with an
accuracy for which there can be no authority or excuse ".   If
archaeological and tree-ring evidence are in conflict, he would al-
ways rely upon the archaeological.

The pendulum of climatic investigations has likewise swung from
one extreme to the other.   All the trees of a region record the lean
and the fat years (Davis, 1931); naturally we would like very
much to know how and why.   The idea that growth is largely de-
pendent upon annual precipitation came as an inspiration (Haw-
ley, 1939).   To many people a 500-year record of weather derived
from tree rings was not only astounding but " smacked of witch-
craft " (Abbott, 1946), and the evidence of weather contained
therein was as irrefutable as fingerprints.   A simple statement,
however, that a thin ring means a dry year and a thick one a wet
year is perhaps a bit over-simplified (King, 1951).   " The rela-
tions between growth and climate are . . . perhaps not always as
direct as we are often apt to believe " (Hustich, 1949).   Weather
undoubtedly influences tree growth, but our ability to analyze that
growth may not as yet permit us to read an " accurate history of
weather for centuries past " (Science Digest, 1950).   If growth
can not as yet be analyzed with unfailing accuracy, it is somewhat
premature to suggest that weather may be predicted for " decades,
even centuries, into the future ".   This is especially interesting
when we are told that ordinary methods of weather forecasting pre-
dict one or two days in advance, and then only with something like
50 per cent accuracy.

In contrast to the above statements, Friesner (1943b) frankly
pointed out that " there still remain today a number of unsolved
problems " having to do with the relation of climate to tree growth.
Hustich (1948a) discussed annual alternations of various types of
growth dependent upon climate: " We must, however, have a
deeper knowledge of the physiological processes in the shoot de-
velopment and of the awakening of the cambial activity to under-
stand the true relations between climate and growth ".   A year
later he said that no correlation existed between tree-ring series in
Alaska and in Scandinavia or even between series in continental

Lapland and on the coast of Norway because they are in different climatic regions: " In this respect the importance of dendrochronology has been highly overestimated ". A more hopeful note is sounded by Brier (1948) : ". . . it seems appropriate to endorse the closing remarks of Jones (1947) to the effect that the investigation of trends of growth shown by trees over long periods (as distinct from the attempts to interpret the peculiarities of individual rings—Jones) offers a promising field of work for the climatologist studying long-period fluctuations in the world's climate ".

Thus claims have been made both in chronology and in climate that are somewhat extreme. Words of caution have appeared from time to time. But our greatest concern is not with the extravagance of the claims in themselves, claims encompassing accurate dating to the year of tree growth 19 centuries in the past and substitution of tree-ring thicknesses for weather records not only centuries in the past but also centuries in the future. Our concern is rather with the suggestion of final accomplishment and dogmatism in certain methods, in mathematically restricted statements and in sharply delimited classifications which, if unchallenged, would reduce further inquiry in several fields to mere routine and blight the spirit of research in student and experienced investigator alike. In any event, be the claims valid or not, we may perhaps be forgiven if we prefer the zest of uncertainty and discovery among the biological variables inherent in tree growth rather than case-hardened finality in our results.

GROWTH AND GROWTH FACTORS

THE FACTOR COMPLEX

Botanists for years have realized full well the highly complex array of factors which influence tree growth (i.e., Brown, 1915; MacDougal, 1923), and some have done detailed experimentation with one factor alone, e.g., soil moisture (Veihmeyer, 1927). Such realization and experimentation have given us a clearer overall picture of the problems of tree growth than a host of correlations between growth and a single factor. More and more, however, all workers have become impressed with the multiplicity of factors, the complexity of their inter-actions, and their detailed areal variability.

The statement of Daubenmire (1948–49) may fit the problem of growth factors: " It is clear that no one factor can be used to ex-

plain all variations in the phenology of all plants. It also seems safe to state that, although certain general principles may apply to many plant species, deductive inference will never permit accurate prediction of the ecologic relations of particular species that have not yet been the object of special study ". And for such study the fundamental work of Pearson (1950) over many years must point the way. The analysis of climate alone is, according to Brooks and Kelly (1951), a very complex task, and no less complex is the study of vegetation and soils because they are " mirrors of the normal climate of a region " (Hare, 1951). In the words of Watt (1943) there is " need for a dynamic conception of forest ecology. The pattern of the forest plantation must be determined by a variety of causes: microclimates, soils, relations between one plant and another, and the structure of the vegetation; the organic factors of the environment being no less important than the inorganic ". It is conceivable that secular trends in radial increments can be brought about by release of one kind or another, by reduction of crown, by periodic pest attacks, by fruiting or by variations in competition. Shirley (1945) reviewed the problems of light as an ecological factor. His study " further emphasizes the desirability of seeking through factorial design of experiments and multiple correlation analysis, to work out the true interrelationship of the several growth factors of plant habitats. To confound them with one another inevitably confuses thinking, thereby adding mystery to subjects open to clear analysis ".

Many workers call attention to the multiplicity of factors; a single phrase in each case illustrates this: " complexity of the processes concerned with the water relations of plants " (Broyer, 1951b); " complexus of factors concerned with . . . water movement into plant systems " (Broyer, 1951a); " width of rings . . . determined by a complex of interacting factors " (Gladwin, 1940a); " it is . . . readily seen that diametral increase is not controlled by any one factor of the environment, but by a combination of factors " (Friesner, 1941); " for the thickness (of tree rings in the climate of Potsdam, Germany) depends on a number of factors often independent of climate " (Meissner, 1943); no one factor controls fruit production, " rather a complex of factors " (Pearsall, 1950); " apparently so many factors having an important bearing on the total growth (of coast redwood) that correlation with any one of them

is not feasible " (Schulman, 1940*a*) ; " tree growth depends on many factors " (Hawley, 1941) ; and " growth of young trees depends upon a complex of factors" (Vegher, 1946). Kramer (1948) goes a step farther and relates tree growth not only to environment but also to heredity.

The difficulties of observing all factors at the same time or even of measuring more than one are rather great. However, such attempts have been made by Gustafson (1943), Hustich (1948*a*) and Kaufman (1945).

In relation to growth and growth layers specifically, the views of several workers should be given. Turner (1936*b*), who worked in Arkansas, emphasized the role of soil and topographic features, not neglecting the " possible effects of differences in the climatic complex " on height growth. The rate of such growth, however, " cannot be correlated with any single factor, but rather is dependent on the interaction of several factors ".

Friesner and Friesner (1941) recognized the importance of all factors on the formation of annual rings. Although some factors are internal and hereditary, whereas others are external and environmental, " variations in growth . . . from year to year within the same individual are related more definitely to environmental than to internal factors ". Temperature and light among the external factors are commonly adequate for growth, and available water commonly is the limiting factor. Thus " growth curves of trees will more often show a relation to rainfall curves than to those for any other single factor ". But rainfall used alone has its problems because " the relation of growth curves to rainfall is not a simple one. Such factors as the following enter to make the relation complex : the time of year when the rains come, the proportion which comes during the growing season, how well they are distributed over the growing season, the topography and its relation to runoff, the character of the soil and its ability to store water from times of abundant to times of inadequate rainfall ". The storage of water depends upon climate, depth and nature of the water table, and the local geology, in relation to the root habits of the trees concerned. It may be more a matter of food manufacture and storage than of water holdover. Later, in 1950, Friesner stated that he is " dealing with a complex of variables and the degree of relationship of any one of them with growth will be modified by the others ".

Hanson in 1938 fully recognized the factor complex. In addition to climate, he found that disease, insects, animals, fire, lightning and competition have an influence on growth: " Thus it is not always prudent to base small annual rings or variations upon climatic conditions ". He further emphasized the complexity, in 1941, and discussed even more factors, but, since " climate is probably the most unstable factor of the environment, it is only natural to expect some correlation between climatic fluctuations and tree growth ". There are, nevertheless, many characteristics of rainfall and soil which in part determine the amount of soil moisture present when trees need it. Therefore " it is apparent that the total rainfall in an area is not necessarily an index to the amount available for tree growth ".

In a review appearing in 1941 Pearson remarked that " the erratic behavior of growth curves in relation to climatic records is well known to foresters and ecologists in this country who have attempted such correlations ". Pearson himself kept records in the midst of the trees he studied and repeatedly (1950) emphasized the multiple nature of growth factors. A striking contrast to the remarks of Pearson appeared in the statements by Lyon (1949) who worked in New England. He points " to the accumulation of considerable evidence that the secondary growth of many conifers is determined to a large degree by the water supply available to their roots during the growing season ". Therefore he offers the following: " When the annual growth increment does not agree well with the precipitation record, the relative ring width is a better index of the water supply available to the root system than are the records of weather bureau stations, due to the complexities of runoff, evaporation, interception by crowns and water holding properties of soils ".

A close view of the work being done with growth layers nourishes the hope that fundamental investigations will more and more come to the front. Such experimental work as that of Blackman and Rutter (1950) on light and nutrients or that of Went (1949) on growth in an air-conditioned greenhouse points the way to us in growth-layer studies. " In the field the plant is never subjected to a single variable " (Went, 1950).

Chowdhury, working with growth rings in India (1940), was not able to assign " growth activity to any particular factor ". Millet (1944) studied the growth increments of Monterey pine in

Australia in relation to rainfall and concluded that " the problem of growth of a forest and climate will not be near to a satisfactory solution until much more of the environmental complex is taken into account ". Working on hemlock, Meyer (1941) said that " it remains an unsolved question what meteorological factors or combination of factors influence the annual growth of trees in northern Pennsylvania, where rainfall is not a limiting factor ". A very similar conclusion is stated by Friesner (1943*b*) : " The problem of sorting out the different factors of the environment and determining just what role each plays in the matter of growth is well nigh unsolvable because the behavior of the individual is its response to its total environment ". Byram and Doolittle (1950) worked on the growth of shortleaf pine of the South from the standpoint of silviculture; their remarks perhaps apply equally well to growth studies in general. In respect to radial growth they say that " it is not possible to designate specific factors as having dominant effects on tree growth. Several factors seem to share the leading role in regulating radial growth rate, and the position of most importance alternates from one factor to another ". They therefore suggest a possible remedy: " The progress of silviculture and forest management will probably be greatly accelerated when there is more basic knowledge on the physiology and chemistry of the individual tree and the components of its environment. To understand the tree as an individual may be the most important step in ultimately understanding and predicting its behavior in a stand ". Such surely must also apply to problems of ordinary annual growth. Lutz (1945) apparently agrees, for he wrote: " To the reviewer the need for experimental investigation of the relations between width of tree rings and climate, soil, and competition seems particularly urgent. In other words, we need more precise information on the relation of diameter growth of trees as influenced by environmental conditions. With information of this character available the possibilities of dendrochronology will be very great indeed ". The lack of experimental and observational work on tree growth has also been emphasized by Glock (1942a).

FACTORS AT A PARTICULAR SITE

FUNDAMENTALS. During the past decade botanists have continued their fruitful studies of individual growth factors in relation to growth, on the one hand, and to the multiplicity of factors, on

the other. Many studies illuminate the path of future investigations and at the same time neither obscure nor obstruct the biological complexity of the problems involved. In citing a few examples there is no intention of emphasizing their merits over many others: the calculation of growth in relation to age and vigor of pine, by Briegleb (1945) ; the stem analyses of Burns and Irwin (1942) ; the detailed growth of a single pine for a year, by Byram and Doolittle (1950) ; the effects of defoliation, by Church (1949) and by Baker (1941) ; the speed downward of soil-moisture percolation, by Colman and Bodman (1944) ; the relation of stream flow to precipitation in a semi-arid drainage basin, by Cooperrider and distribution of rainfall, by Darrow (1943) ; the time and rate of Sykes (1938) ; the relation of ocotillo growth to the amount and radial growth at different altitudes in relation to variations of temperature and rainfall, by Daubenmire (1945–46) ; a comparison of growth characteristics in deciduous and evergreen trees, by Daubenmire and Deters (1947–48) ; the studies of elongation and diameter enlargement, by Friesner (1943*b*) ; growth measurements on leader, needle, cambium and root, by Kienholz (1934–35) ; the growth response of pine in bog and upland of humid New England, by Lyon (1949) ; the lucid analysis of the forest-tundra ecatone, by Marr (1948) ; the comprehensive and fundamental studies of ponderosa pine over the years, by Pearson (1950) ; axial and radial growth habits of deciduous trees in Indiana, by Reimer (1949) ; the analysis of growth factors in Arkansas, by Turner (1936*b*) ; diameter growth of Monterey pine in relation to rainfall intervals in Australia, by Fielding and Millett (1941) ; the microclimatic studies of rainfall, by Linsley and Kohler (1951*a, b*), and of temperature, by Shanks and Norris (1950) ; the detailed experimental work on soil moisture, by Veihmeyer (1927) ; and the specific time of growth, both axial and radial, in relation to measured soil moisture, by Watkins and de Forest (1941).

These examples illustrate the value of prolonged observation, detailed measurement and controlled experiment to the problems of growth and the factors which control that growth. Many, if not all, of these studies are fundamental; they are part of the groundwork which eventually will give us a better understanding of the physiology of growth and of the xylem increments set off by cambial activity.

In spite of close analysis of some one growth factor, botanists have seldom lost sight of the complex of interrelated factors. The effects of drought, temperature and sunshine can scarcely be separated, or those of drought and insect attacks, or of fruiting years and rainfall. However, an attempt has been made to meet the difficulties by using, for instance, controlled conditions or by experimenting with one or two factors while the others are near optimum. As a result we have today a far more lucid picture of growth than 20 years ago because of the painstaking studies of botanists, foresters and horticulturists. A reference to all such work would go far beyond the scope of the present report. We would, nevertheless, be remiss if we did not mention a few who have analyzed a single factor while cognizant of the entire complex. Among these there are the works of Briegleb (1945, 1950), Byram and Doolittle (1950), Friesner (1941, 1943a, b, 1950), Friesner and Friesner (1941), Gladwin (1940b), Graves (1946), Hansen (1938, 1941), Huber (1948), Hursh (1948), Hustich (1948a), Marr (1948), Moseley (1941), Pearson (1950), Schulman (1945b), Shirley (1945) and Zeuner (1951a). Only under controlled conditions, guided by our experience, can we be reasonably certain of the exact effects on growth of the variations of some one factor. And we must be reasonably certain of our knowledge before we assign a single cause operating unobserved in the past to the production of a certain amount of xylem in contrast to an earlier or later amount.

LOCALIZATION OF FACTORS. The problems connected with growth in general or with discrete increments have been approached by two methods, the one having to do with the individual tree, the other with groups of trees. As regards the single tree in its highly localized environment, a relatively few studies in micro-ecology or microclimate give strong emphasis to a surprising amount of variation among many of the factors within short distances, both vertically and horizontally. Perhaps this, as well as internal differences, helps to explain why two trees which are separated by a few yards can respond somewhat differently in cambial activity and in the formation of xylem.

As regards groups of trees, many studies have been made in an attempt to measure or interpret growth response in relation to a factor general in its effect over the area. Two problems arise immediately. The first pertains to the universality of growth re-

sponse over an area. Some workers use practically all the trees, whereas others exercise high selectivity, even going so far as to reject by a two-fold process all except the slightest fraction of the entire stand. Selection, for instance, to avoid the effects of competition where the study of competition is not the desideratum, or to avoid a superfluity of repetitive data, may be entirely justified; but the rejection of trees, initially selected with care, because they do not conform to a subgroup within the larger group may give rise to serious questions. Which small subgroup out of a well-selected collection from a stand represents the growth factor being studied? Can we in the laboratory justifiably choose 10 to 20 per cent of the specimens out of a collection well-selected in the field and, because the growth-layer sequences have a certain type of similarity, hold that the small per cent records, say, the variations of rainfall? What do the other 80 to 90 per cent record? Which species records some one factor if each of two subgroups in a stand consists of one species conformable within itself but not conformable between the two? These questions are not rhetorical; they actually have come up in work with growth layers.

The second problem dealing with growth response concerns enlargement of the area. As the area of growth response expands, it is reasoned by some that factors operating locally lose their significance, and when hundreds of square miles are included, only an overall factor of most general effect exerts a uniform influence at widely separated time intervals. Such a factor might be the average temperature of the growing season, which could be sufficiently uniform over a large region to effect the growth of at least a portion of the trees a sufficient number of times during a century to permit correlation of those effects among the particular trees. However, even temperature fluctuates locally to a rather high degree, and the problem arises as to which trees represent the regional index and where they are to be found. Are they the trees whose growth responses measured by amount of wood formed are similar? And, if so, what are we to do with two or more sets of correlation from the same region? How can we as plant ecologists interpret the responses of the remaining trees? Since responses in respect to the amount of xylem formed can vary only in a three-way fashion—alike, unlike, or neutral—the results of chance correspondence must be eliminated from the measurements. The

value of finding a regionally integrated temperature gauge, or the like, is so great that no effort should be spared to carry on the work. At the moment the picture is none too bright, and methods employed should be critically examined by plant physiologists, ecologists and meteorologists.

An examination of the work done gives an idea of the trend of thinking. First perhaps we should examine what has been done about purely local factors, as in the area covered by one tree, and then pass on to individual factors over larger areas. Hursh (1948) used local climate in a slightly broader sense than many of us use microclimate. He measured air and soil temperature, wind, evaporation, air-moisture-saturation deficit and rainfall of three contrasted zones—bare, grassland, and grass and trees merging into forest in the Copper Basin of southeastern Tennessee. Two sets of three stations each crossed the zones, one set in a rough line less than eight miles long, the other in a line four miles long. Each zone, Hursh found, contained " a distinctive local climate ", and each factor which he measured varied appreciably from one zone to another.

Shanks and Norris (1950) also worked in eastern Tennessee, on microclimatic variation in a small valley. They recorded temperature differences on north- and south-facing slopes, and the variability, seasonal trend, frost pattern and actual freezing damage at seedling level. Across the small valley the mean temperature differed by 3° F. The minimum temperature from ridge top to valley bottom differed by 6.4° F. There existed a difference of 20 days in date of the first killing frost. Thus differences do exist within short distances, differences that can affect growth.

In 1946 Ives wrote about diurnal air circulation in valleys in relation to the difference in altitudinal ranges of various species from valley to valley. Much of the variation remained unaccounted for, even after corrections were made for gross climatic conditions, effective daylight, available soil moisture and soil chemistry. This work of Ives illustrates another complexity that is local and can conceivably cause differences in neighboring trees.

Observations at Neotoma, a small valley in central Ohio, by Wolfe, Wareham and Scofield (1949), revealed great differences of temperature within one mile. In a frost pocket of the valley the minimum temperature on a certain day was — 25° F., whereas

within a mile in the nearby woods beneath leaf litter the temperature was 29.5° F., a difference of 54.5°. Such a variation resembles that of tens of degrees of latitude or thousands of feet of altitude.

As described by Parry (1951), a thin hot layer of air heated by the sun lies close to the ground where it is bare. Where vegetation exists, the heated layer rises " to a height which depends upon the height and density of the vegetation ". Is it possible that such temperature differences could have an effect on physiological processes at different elevations in a tree?

Linsley and Kohler set up a network of 55 rainfall stations two miles apart to measure variations of rainfall during one storm (1951b) and during two intervals, April 29–September 21, 1947, and February 5–September 22, 1948 (1951a). The network was in the form of a rectangle five stations in width and 11 in length. In one storm of heavy rainfall from August 4 to 7, 1947, there was a high degree of variability ranging from about 0.2 inch to 3.4 inches. Neighboring gauges differed by as much as a factor of three. Over the longer intervals of time, areal variations in rainfall, although present, were relatively less than for a single storm. One line of gauges, each two miles from the other, gave readings in inches as follows: 43.2, 47.4, 50.9, 44.9, 51.4, 46.1, 55.8. Two other sets of two, two miles apart, gave 46.2, 53.0 and 47.2, 55.5 inches. In spite of these variations " extremely dense networks are not required if the occurrence of an occasional large error is not serious . . . a relatively sparse network can be utilized to determine regional precipitation characteristics ".

With respect to tree growth these highly local variations, as in rainfall, may account for the differences not only between adjacent trees but also between groups of trees. Variations in one factor, furthermore, added to those of other factors, create a complex situation which, it would seem, can be resolved only by detailed micro-ecologic studies. Then we may understand why the relative and absolute amounts of xylem formed in two adjacent trees resemble each other or differ, or why two trees remote from each other correlate and two close together do not. Statistical manipulation appears to have been called upon occasionally in order to attempt elimination of certain growth irregularities. Perhaps Schulman (1951) has actually removed a portion of the influence

of micro-ecologic factors in partly removing what he calls the random term in growth of each tree by elimination of age trends. Environmental and genetic influences aside, can we have such a thing as a random term in tree growth? Giddings (1941) made an interesting comment about what may be construed as local factors when he said: " A long ring record carries enough dating characters common to the whole area to overcome misleading local aberrations ".

RAINFALL. The unintentional confusion resulting from use of the word " climate " rather than some one element thereof has largely disappeared. A few cases do exist (Giddings, 1941; Hawley, 1941; Schulman, 1942*a*, 1945*b*, 1951), probably because of the desire to obtain variety in words. However, it is confusing and may be misleading to read the word " climate " and find that rainfall, or temperature, or some other factor is actually intended. One does not wish to read into a statement something not intended. For instance, heredity and environment, which cannot be clearly separated in nature, " govern the significance of ring-width series as climatic records " (Schulman, 1945*b*).

Students have come to " realize the difficulties of designating a single environmental factor as chiefly controlling one or all growth responses " (Sampson and Glock, 1942). Substitution of growth-layer thicknesses for rainfall records is no doubt an ambition of ideal proportions, but as yet there is no substitute for the standard method of emphasizing one variable while holding the others constant or, in the case of individual trees, selecting them so that the other factors have nearly the same impact on each tree. A majority of the workers in growth layers do emphasize one or more factors while at the same time recognizing the actual multiplicity of factors.

Because of the importance of water in our economy, it is only natural to seek all possible information on rainfall. Briegleb (1950) noted that wide periodic variations in rainfall and corresponding variations in tree growth characterize the ponderosa pine type. Although he emphasized rainfall, he was " aware that the rate of growth that occurs on a given site may vary widely, depending upon the genetic characters of the growing stock ". Vigor, crown size and site have great influence on growth. During unfavorable periods low-vigor trees experience a greater reduction in growth

than do high-vigor trees. Among trees with good crown-vigor it is the older age classes which have the greater relative decline in growth. Trees on poor sites react to precipitation cycles by variations of increment in a more pronounced fashion than do those on good sites. Thus it is patent from the work of Briegleb and other foresters that more or less violent fluctuations in growth increment are to be obtained from low-vigor trees of younger ages, from good crown trees of older ages, and from trees on poor sites. Even so, growth also depends upon the genetic character of the stock. These low-vigor poor site trees yield growth-layer sequences designated as variable by botanists and foresters and as sensitive by several of the tree-ring workers. The one term is descriptive, the other interpretative. Physiological investigations on growth and growth factors will in time indicate whether or not the selection of the term " sensitive " was a happy one.

Rainfall and temperature are treated as mutually interacting factors by Byram and Doolittle (1950) in their study of the Southern shortleaf pine, although they maintain in general that " it is not possible to designate specific factors as having dominant effects on tree growth ". During the spring, growth was at a maximum when light, moisture and temperature were at an optimum; limiting effects may have been exerted by available nutrients, or by inherent characteristics of the trees, or on warm sunny days by a transpiration rate greater than the vertical transport of water, even with an excess of soil moisture. Stored soil moisture decreased in June, and from then until August soil moisture was a limiting factor on radial growth. Prolonged drought induced shrinkage of tissues, and " the length of time for recovery following a rain seems to be determined only by the time required for the water to reach the roots ". This study by Byram and Doolittle of a year of detailed growth in the life of a single shortleaf pine may serve perhaps in its biological approach as a decided contrast to other studies with a mathematical approach.

In a very straightforward fashion Dale (1947) described the hot winds and the uncertainty of rainfall on the Great Plains which, after all, are similar to a lower forest border except that climatic conditions are more extreme and fluctuations more violent. Darrow (1943) studied the growth of ocotillo and found that " the amount and frequency of terminal branch increment vary with climatic

conditions and with the general age of the individual plant or branch ". Vegetative increments depended upon amount and distribution of precipitation. As a rule, terminal growth occurred during the summer rainy season and only occasionally in spring. The size of the branch increments likewise seemed to depend more upon the amount of summer rainfall than upon that of spring. A very low summer rainfall after a moderate spring rainfall gave a minimum of active branches and a minimum amount of growth.

In southwestern England Dobbs (1942) studied ring patterns in larch which is rarely subjected to a condition of limited moisture. This is modified somewhat, however, by the conclusion that " the number of false rings appears to vary inversely with soil depth ". Certain narrow rings did correspond to drought years, but on the whole even trees on the same site failed to give a uniform pattern of growth. Under the conditions in southwestern England many local patterns existed in conjunction with certain regional similarities. It will be interesting to learn how well growth-layer thicknesses correspond to rainfall in view of local differences and regional similarities.

Douglass (1945, 1946b) strongly emphasized the role of precipitation in the southwestern United States, although, as will be seen later, he relied strongly upon steep slopes and thin to patchy soils as controls for tree selection. Thus lower forest border conditions were highly accentuated and even completely atypical in so far as moisture conditions on a normal site were concerned. This insistence on atypical factors at a particular site should be contrasted with the work of Lyon (1943, 1949), Friesner and his coworkers (1941, 1950, etc.), Dobbs (1942), Glock (1950) and others who found correspondence between rainfall and tree growth, not in the extreme lower forest border but in the forest interior. Douglass (1946b) in photographs contrasted complacent and sensitive ring records: " In our dry country, complacent ring sequences . . . indicate that the tree is getting sufficient water and does not respond to changes from year to year ". Would this lack of change, then, indicate that all growth factors are in perfect balance and near optimum in relation to each other year after year? The botanical and ecological implications of the quotation bear so many facets, aside from the terminology used and the principles of geographic distribution of species, that a complete discussion is im-

practical. If the ring sequence actually is completely uniform ("complacent"), then the tree must have had an optimum amount of water, never too much, never too little, for uniform yearly growth—constant water supply and no long-continued submergence of all roots.   Such a site would, in our experience, be atypical to the ponderosa pine zone.   Drought in humid regions affects the trees native to the region just as it does trees native to dry regions.   Such instances were the death of beech during drought in Ohio and defoliation of trees in the District of Columbia during a hot dry spell.   The capacity of trees to respond to changes of one kind or another in the environmental complex can hardly be expected to be confined to the trees growing along the edge of the desert in the Southwest.

In Australia Fielding and Millett (1941) studied diameter growth of Monterey pine by means of the dendrometer under two different climates, the one a dry upland with irregular rains and the other a more favorable forest climate with seasonal rains. Distinct diameter growth in the dry upland occurred only during spring; but growth always followed soaking rains of summer and autumn.   Under the forest climate there were two main periods of growth, spring and autumn.

Friesner (1950) studied the effect of rainfall on six species of hardwoods in Brown County, Indiana, and concluded that the particular site played an important part in the relation of a tree to rainfall.   In 1941 Friesner and Friesner had studied the relation of ring growth to rainfall in six species of hardwoods from Marshall County, Indiana, and found that during the normal growing season available water became the limiting factor while temperature and light were commonly adequate.   The bare rainfall figures for any single interval did not always correspond closely to growth—the condition of the soil, the amount of runoff, and the nature and amount of rainfall in the months preceding the growing season were modifying factors.

Giddings (1941), working in Alaska, held that trees reflect climate if the relative thicknesses of the respective growth layers correspond from tree to tree.   This visual correspondence was called "crossdating".   Later Giddings restricted the climatic control to that of temperature.   Complacent sequences mixed in with sensitive were difficult to explain on a temperature basis.   Because

the river-bottom trees agreed among themselves but varied from the record at timberline, Giddings interpreted the difference as a disturbance due to local conditions of slope, stream action and ground cover. If temperature is a major factor in the Northlands, and it seems reasonable, we wonder what a detailed study of temperature stratification, temperature inversion and altitudinal effects would show.

Rainfall records, in contrast with those for soil moisture, for instance, are comparatively easy to gather. What trees, from what zone, growing under what conditions record rainfall to the greatest extent? Glock (1950) took his trees from the forest interior—upper part of transition zone in northern New Mexico—and related growth to rainfall. Hansen (1941) related growth to rainfall in trees from near the lower forest border in central Washington where " precipitation is probably the chief limiting factor in the growth of trees . . . and the nearness of the timberless zone indicates the presence of unfavorable conditions ". Thus conditions are below optimum especially as regards temperature and rainfall: " It is apparent that the total rainfall in an area is not necessarily an index to the amount available for tree growth, of which radial increment is a function. The time, the amount, intensity, type, and frequency of precipitation, in conjunction with the depth, porosity, water holding capacity, and structure of the soil, and the topography, control the amount of water retained. Once the water is in the soil, the temperature, the H-ion concentration, structure, and texture of the soil further control the amount of water available for absorption by the plant ". This summarizes at least partially the extent of the problem that concerns ecologic factors at a particular site and perhaps should be compared with the statement of Hawley (1941) that for her purposes in a large area centering in Tennessee it is sufficient to know a tree's location within 50 miles: " The tree-ring areas have been found to be so large that this approximation of location is close enough for all the work except that of special botanical and ecologic interest in giving the exact reaction of a tree to its surroundings . . . since the major interest of the laboratory so far has been cross-dating trees and extending charts, the data regarding geography and location within the fifty mile radius has been sufficient ". Although these statements have been criticized by Glock (1942a, b), they should be compared, first, to the work of

Lyon (1943) who found areas of homogeneous growth to be much more restricted in New England than Hawley did in the eastern part of the Mississippi drainage basin, and should be compared, second, by the individual botanist with his own ecologic work. Miss Hawley studied trees grown under a rather humid climate and related their growth to rainfall and temperature.

Kapteyn (1914) in western Europe and Lyon (1943) in New England considered water supply as governed by rainfall to be the dominant factor in tree growth. Apparently trees growing at the edge of the desert are not alone in recording rainfall. Although Lyon found growth resemblances in extreme years up to a distance of 50 miles, he said that " The fluctuations in the values of the mean ring widths from year to year are . . . due to environmental factors at the site, chiefly those of climate because the edaphic factors are fairly steady in a forest in relation to the dominant climate ". In an interesting comparison of bog and upland pine in New England, Lyon (1949) found that in their growth on the two sites the trees had strong similarity to each other, contrary to what one would expect. Rainfall combined with release is the factor of greatest influence on both upland and bog trees.

High temperature combined with moisture deficiency killed feeding roots of jack pine (MacAloney, 1944) and brought on severe decadence. Even though budworm defoliation did not directly cause death, it helped in the final stages: " The death of the trees was very probably due, in the final analysis, to the drought in 1938 and 1939 ", which terminated 20 years of drought or near drought. But it should be noted that under the drought conditions only the poorest trees decreased their growth in basal area, whereas the best trees increased their growth.

Pearson (1950) has given us a fundamental analysis of the effect of site factors on the growth of ponderosa pine in the southwestern part of the United States; in fact his work is so fundamental that a deserved résumé of it would go far beyond the limits of available space. He emphasized the interacting complexity of growth factors —soil moisture, temperature, light, release, rooting and soil. Even so, " competition for the limited moisture supply dominates the whole ecologic picture ". What Pearson's work means to the forester and ecologist is illustrated perhaps by his attention to details affecting trees at particular sites. The opening of crown canopies

in dense groups at Fort Valley, Arizona, could increase the total precipitation reaching the ground by as much as 40 per cent. Such an event combined with the fact that " large trees as far as 200 feet apart may possibly send their roots into a common zone " gives us something to consider when we attempt to interpret the reasons for variation in xylem increment in the past; that is, growth variations may be caused by factors other than climate or climatic cycles.

In a series of papers Schulman (1940a, 1942a, 1943, 1945a, b, 1947a, 1951, 1951–52a) stressed the relation of growth to rainfall in saying that trees act as natural gauges of annual rainfall (1945a) if they grow under extreme conditions of the lower forest border. Extreme emphasis on the water factor served, it seems, to mask the effect of other factors. The habit of selecting trees whose water relationships were abnormal has been carried over to Arkansas (1942a), but discrepancies between growth and rainfall crept in and were caused by disturbing factors. Although rainfall was emphasized by Schulman, he tested for temperature relations and recognized many of the physical problems connected with a complex of factors.

Weakley (1943) in western Nebraska gave his attention wholly to the rainfall-tree growth relationship among softwoods which grew well above the dry washes.

TEMPERATURE. For some reason students who work with growth increments pay less attention to temperature effects or have less success with them than with rainfall. Precipitation is measured from interval to interval, but temperature is taken for the most part as minimum or maximum. If perhaps the amount of temperature (or heat) could be measured quantitatively from the time growth begins until it ends (and these dates vary from tree to tree), we might have better success in relating specific tree growth to temperature. Some references to temperature have already been made; for the most part, workers who consider temperature do so in conjunction with other factors.

Daubenmire (1945–46) measured radial growth of trees at various altitudes in Idaho by dendrometer and found growth related to the interaction of temperature and soil moisture modified by altitude. High temperature aided growth if soil moisture was available. In a later study, Daubenmire and Deters (1947–48)

measured the growth of deciduous and evergreen trees at Moscow, Idaho. No tree was native, but all had become adjusted. Of major interest to them were the relationships of temperature, soil moisture and soil temperature to growth. Although dendrometers may not give us a perfect record of growth, the basic work of Daubenmire and Deters does seem to cast a measure of light on certain growth characteristics.

The same may be said for the work of Friesner (1941, 1943a) who studied growth in the beech of Indiana by the dendrographic method (1941). He related growth chiefly to temperature and soil moisture but discussed other factors as well: " The most important external factors controlling wood formation which are variable on the same site from season to season and day to day are temperature, evaporation rate, and available water ". Probably temperature was a limiting factor early in the season when water was available and water became limiting later when temperature was adequate: " The relation of these factors is not a simple one . . .". Friesner's study of elongation (1943a) perhaps emphasized the role of temperature because the period of observation was shortened to a day or so. The present writer has daily observations of tip growth on fruit trees in Maryland. These showed a close correspondence between temperature and tip growth while tip growth was in active progress.

Giddings (1941) worked with trees in northern Alaska where water supply was adequate during the short growing season. Growth took place during the longest days, days of greatest solar energy. Temperature and altitude had a fair relation to growth, a relationship which brought in complications because cambial division occurred at different times at different places in such a fashion that ring thicknesses did not match. If other factors such as altitude, soil moisture and soil could be held more or less constant, it might be that xylem increment would be found to correspond to some aspect of the temperature regime in air or soil during the interval of greatest physiological activity. Since a priori logic suggests that temperature is an important, or near dominant, factor at high altitudes and high latitudes, one hopes that Giddings and other high latitude students can resolve some of the complexities and thereby clarify the temperature relations, should such actually exist.

Studies on tree growth in northern Europe are perhaps well illustrated by the work of Hustich (1948*a*) in Finland where temperature appeared to be the factor of paramount importance, and great differences in altitude did not complicate growth reactions to the extent that they did in Alaska. Hustich, however, did not consider temperature exclusively; he found relationships with wind, light, flowering and fruiting. For instance, " The wind is . . . a climatic factor which in the polar regions is hard to distinguish from the low temperature ".

SOIL MOISTURE. Tree growth depends not so directly upon rainfall as upon the soil moisture present and available at the time when that growth can and does occur. Mr. C. K. Cooperrider, in conversation during a ride across the dry lands of southern New Mexico some years ago, mentioned the prime importance of the role of soil moisture in tree growth and suggested that students of growth increments would be striking closer to the heart of their problems if they measured the fluctuations of soil moisture instead of using rainfall records in tree-growth comparisons. No one can deny the importance of the suggestion. But rainfall records are, so to speak, ready-made for our use, whereas the collection of soil-moisture data entails laborious sampling at very short intervals over a period of years. We await the means and personnel for such a project. In the meantime we are aware of the acute desire to find a shortcut method for the revelation of meteorological records of the past in tree rings. Such desire has been shown by the following expressions: " indices of past winter rainfall " (Antevs, 1948) ; " accurate history of weather for centuries past " (Science Digest, 1950) ; " centuries-long histories of precipitation " (Schulman, 1943) ; " natural gauges in trees which have been continuously recording fluctuations in annual precipitation " (Schulman, 1945*a*) ; and " precipitation records from tree rings " (Will, 1946). In contrast, Friesner (1941) tells us that diameter changes reveal an immediate and close relation to available moisture, as shown by the irrigation experiments of MacDougal. The work of Friesner and MacDougal does not lend itself to such spectacular phrases as those listed above, but one feels that in the long run botanists and foresters will have more confidence in work of such caliber.

Much work has been done on soil moisture, per se, and inter-

related factors. Soil scientists have made great contributions as have also the men and committees whose work has been reported in the Transactions of the American Geophysical Union. Because so much work has been done it would be impractical to make a complete report; a few illustrations only will be given. He who would approach the problems of tree growth intelligently and understand some of the fundamentals underlying the growth layers which he uses, must know something not only about soil moisture but about the soils themselves. If and when facilities are available, tree growth must be studied in relation to soil moisture which in turn must be studied in relation to rainfall.

Colman (1944) studied field capacity in relation to depth of wetting. Field capacity, he said, was considered to have been reached two or three days after irrigation in well-drained soils of at least moderate permeability. In fact, any rapid changes in soil moisture must have occurred in the first 24 hours. Obviously the speed by which wetting occurs, field capacity is reached, and capillarity, evaporation and transpiration are carried on, helps to determine how much soil moisture is available for tree growth and for how long a time. This impinges directly upon food manufacture, food storage and so-called lag effects which are discussed by some students of tree rings where the thicknesses of two growth layers of the same date in different trees do not match or where a growth layer seems to match the rainfall of a previous year instead of that of the same year.

Information on downward wetting has been expanded by Colman and Bodman (1944) in their study of moist and layered soils by experimental wetting. In air-dry sandy loam, 12.5 centimeters of water penetrated 37 centimeters in 100 minutes. In initially moist soil, 6.7 centimeters of water penetrated 61 centimeters in 100 minutes. Water took about 400 minutes to penetrate 36 centimeters where 14 centimeters of sandy loam overlay silt loam. If the water penetrated to the silt loam faster than it could pass the silt loam, the excess ran down the plane of contact. Such factors at a particular site are not too easily visualized by inspection of the surface alone.

It may not be amiss to refer back to the thorough work of Cooperrider and Sykes (1938) on a semiarid drainage basin in the Salt River area of Arizona. One inch of rainfall commonly pene-

trated less than three inches into badly eroded soils bare of vege-
tation, whereas it reached six to eight inches or more on the same
slope if covered by plants. The end of the winter rainy season and
subsequent depletion of soil moisture came at the time when the
full growing season was inaugurated. Much later, summer rains
revived grasses and other kinds of plants, and even trees and
shrubs with roots near the ground surface were under conditions
favorable for growth.

In addition to the comprehensive summary on soil moisture in
relation to plant growth by Kramer (1944) there are briefer, more
specific reports. Kittredge (1949) measured rainfall in the open
and under trees on 142 foggy days. In the open he obtained 25.19
inches rainfall, whereas under the trees he got 36.42 inches. Thus
drip due to fog came to 11.23 inches which is an average of 0.08
inch per day. Schiff and Dreibelbis (1949) measured rate and
depth of infiltration of soil moisture in eastern Ohio. For the top-
soil or plow layer they found a maximum penetration of ten inches
per hour and below that 0.6 inch per hour.

A person concerned with forest ecology finds it necessary to refer
back to the significant experiments on soil moisture by Veihmeyer
(1927), experiments which bear directly on problems of tree
growth. For instance, irrigation in the dormant season did not
postpone to any great extent the time in the following season dur-
ing which the supply of moisture in the upper six feet of soil was
reduced below the wilting coefficient. Such a conclusion surely
must be taken into account when we seek to correlate tree growth
with precipitation which falls prior to the start of the actual grow-
ing season. Or again, the growth of trees was not influenced by
fluctuations of water supply as long as it fluctuated below maximum
field capacity and above the wilting coefficient. Irrigation water
moved laterally only to a slight extent. Such conclusions bear
directly on the study of tree growth from the forest interior; we
must seek for the reasons for growth variations elsewhere than in a
mere single relation to amount of rainfall.

Oosting and Kramer (1946) found that light and soil moisture
were almost equally important in the survival of conifer seedlings
on the Piedmont Plateau. Two of their observations were: a)
trenching gave better survival and indicated that it depended upon
competition of roots for soil moisture; b) seedlings did get estab-

lished successfully at the edge of openings where soil moisture equalled that of the forest interior but light was better: " Thus, the pines at the margin, which are probably able to manufacture more food and therefore to develop more extensive root systems, can survive drought better than those in the forest. . . . light is probably more significantly controlling than soil moisture in the complex of factors limiting the establishment of shortleaf pine (and loblolly) seedlings under forest stands ".

Many of us feel that Pearson (1950) of the Southwestern Forest and Range Experiment Station understood the ponderosa pine of the Southwest better than anyone else. He impressed upon us constantly the complicated nature of the growth processes and the complex impact of the many growth factors. Soil moisture, temperature, light, wind, competition, release, soils, rooting, damage by squirrels, mistletoe, and the like came under his attention in his study of ponderosa pine: " From seed to sawlog its growth, form, and existence are governed by heat, light, and moisture. . . . Competition for the limited moisture supply dominates the whole ecological picture . . . . Response to release from competition is as universal as competition itself . . .". In his study of light requirements Pearson observed trees in the open and under 50 per cent, 67 per cent and 85 per cent shade. Increasing shade drastically reduced basal diameter and height growth. Small wonder that Pearson expressed to us his distress with the hasty attempts to find a simple one-to-one relation between tree growth and a single factor such as rainfall whose course must trace a devious route, in balance and unbalance among many other factors, through soil, root and stem, and through physiological changes before it can influence the amount of xylem in an increment. Pearson, none the less, emphasized the importance of soil moisture in the Southwest, for " In regions of deficient precipitation, space requirement is primarily an expression of water requirement, although light also plays a part . . . ". Those of us who work with tree growth owe a great debt to Pearson for his report of 1950— we wish we could detail all of the guiding experiments he performed.

Studies by others have been important, even though not so comprehensive as those of Pearson. In North Dakota Will (1946) emphasized the importance of moisture " available to the roots in

the year in which each ring is formed ". In California Watkins and de Forest (1941) detailed the time of growth of some chaparral shrubs dependent upon soil moisture. In Colorado Williams and Holch (1946) studied the zonation into pine, scrub oak and grass, and ascribed this zonation to " the difference in soil texture of the three habitats, together with its effect upon the hygroscopic coefficient, and the resulting quantities of water available to the plants ".

SOIL. Soil without moisture is of no use to plants; with moisture it immediately becomes an active portion of the total environment, chemically and physically, as the single factors alter their mutual relationships. Here, as in the study of other factors, soil as a factor is emphasized but not treated to the exclusion of others. Billings (1950) found patches of ponderosa and Jeffrey pine in the zones occupied by sage and piñon-juniper, at lower elevations under much less rainfall than the normal ponderosa pine zone of the Sierra Nevada. Such islands of pine resisted the invasion of sagebrush because of mineral-deficient soils on hillsides and ridge tops. In east Texas Chandler, Schoen and Anderson (1943) decided that, of all factors studied, soil type proved to be the best indicator of site quality of loblolly and shortleaf pine.

Marr (1948), in his work on the east coast of Hudson Bay, excellently combined a knowledge of ecology and growth-ring analysis. Soil in a broad sense controlled tree distribution; it had no relation to exposure. A considerable diversity of form was related to variations in the type of soil. Growth factors may be grouped as atmospheric, edaphic and biotic, and it is possible to emphasize the effects of the first by proper selection. However, " At the present stage in growth ring research it is not possible to relate ring characters to any one environmental factor ".

Minckler (1943), working in Tennessee, studied the effect of rainfall and site factors on the growth of six species of trees including two pines. Soil-rainfall relationships were complex; the nature of the " B soil horizon " affected the " growth of all species tested except shortleaf pine, and the effect of reduced rainfall is much greater as the impervious quality of the B horizon increases ". In a general way, exposure also influenced growth. All species made better growth on sites with deeper topsoil. Oddly enough, shortleaf pine was not affected by seasonal rainfall, soil consistency,

aspect or depth of A horizon.   Growth was remarkably uniform except with dense vegetative competition.

Paul and Smith (1950) related growth to type of soil and nature of topography.   The more impermeable the soil and the steeper the slope, the greater the runoff and the less water there was available to the roots of the trees.   In an interesting article Roberts (1939) portrayed a simple and direct relation between depth of surface soil and average height of trees.   Soil one inch deep had trees of 2.15 feet; five inches—3.65 feet; ten inches—5.41 feet; 20 inches—8.43 feet; 30 inches—10.83 feet; and 38 inches—12.16 feet.

In the Southwest Schulman (1945b) said the type of soil seems of little importance where it is extremely limited.   This may sound unusual to soil scientists who realize the complex nature of soil genesis, evolution and profile.   But soil was only one factor influencing ring widths in their use for " precise forecasting of climate ", a feat beset by many difficulties, as Schulman emphasized: " Until the physical chain of events, seemingly existent, from variations in solar or other extraterrestrial phenomena to variations in sensitive tree growth is thoroughly explored and understood, this precise forecasting may, perhaps, not be made ".   Perhaps a biological and terrestrial chain of events would be of more intimate and immediate importance to an understanding of growth response in trees.

Storie and Wieslander (1948) studied timber sites at 163 field stations from the Pacific Ocean to the east side of the Sierra Nevada.   In addition to the climatic factor there were four categories of soil factors: depth and texture, permeability, chemical character, and drainage and runoff properties.   The sites for best growth of ponderosa pine, Storie and Wieslander found, need a deep soil (four to six feet or more) of sufficiently fine texture to hold about 12 per cent or more of soil moisture, a permeable profile, an absence of toxic chemicals, acidic reaction, well drained aspect, and an annual rainfall of more than 40 inches.   Poor sites lay generally on the east flank of the Sierra where rainfall varied from 20 to 30 inches and the soil was shallow.

In the same region Stone, Went and Young (1950) studied another facet of the soil problem—the survival of Coulter and ponderosa pine on shallow soils that were often at the permanent wilting point for several months in late summer.   Even so, these

two species apparently survive even though the soil is below the permanent wilting point. The cause is a different matter, for " this ability to survive on soils so dry that some plants die is yet to be explained ". Part of the answer, perhaps, involves what is called " negative transpiration " whereby aerial parts of the trees take up water from the atmosphere.

The work of Turner (1936b) has points in common with that of Minckler and Storie and Wieslander, especially as concerns soil analysis. Turner studied the growth of pine in Arkansas in respect to soil and topographic features. He classified sites into superior, intermediate and inferior, the last comprising extremely gravelly soils on rolling and hilly land, or soils with high sand content on hilly land, or very stony sandy loams with slope of 7 to 25 per cent. In contrast best growth occurred " on soils that are immature, flat, of high silt or silty sand content, with permeable subsoil and hence at least fair drainage but with obviously adequate water supply ". It is worth mentioning that Turner sampled the soils at three or four levels to a depth of 3.5 feet in order to determine, among other things, the physical structure of the A1, A2 and B horizons. In a later report Turner (1937) emphasized the poor quality of the site for pine where mountain soils and steep slopes prevail.

A portion of Burns' work in New England (1944) is of special interest here. His studies on soil temperature and frost conditions in the soil as a plant habitat bear directly on growth initiation, the course of growth and the length of the season, all matters of importance where gross amounts of growth year after year are arbitrarily compared with a single growth factor fixed in time.

RELEASE. Release from competition, whether by natural or artificial means, commonly produces a change in amount of growth. Are we certain of our ability to distinguish a greater amount of growth over several years caused by release, from a greater amount caused by a series of, say, wet years? This is much the same problem as trying to distinguish the slight growth of a heavy seed year from that of a very dry or cold year.

Foresters have carried out many experiments on release from competition by cutting out a part of a stand. In nearly all cases growth has increased for a time in the remaining trees. Favorable growth response has been reported by the following, as examples:

Boggess and Lorenz (1949), working with loblolly pine in southern Illinois; Chaiken (1941), working with loblolly pine in North Carolina; Downs (1946), working with sugar maple, white oak and yellow-poplar in West Virginia and Virginia; Hough and Taylor (1946), working with Allegheny northern hardwoods; Krauch (1945), working with Douglas-fir in the Southwest; Krauch (1949b), working with ponderosa pine in central Arizona; Lyon (1949), working with white pine which grew in bogs in New England; Paul and Smith (1950), working with the several southern yellow pines; Pearson (1950), working with ponderosa pine of the Southwest; Roe (1947), working with ponderosa pine of the Northern Rockies; Steele (1948), working with Douglas-fir of the Pacific Northwest; and Zillgitt (1945), working with sugar maple in the upper Midwest. Thus it seems that increased growth following release from competition is a rather general response among trees.

Release by girdling certain trees in a stand has promoted growth in much the same fashion, as was demonstrated by Bull (1945) in girdling hardwoods among loblolly pine in Louisana, and by Cromie (1945) in the woodlands of Connecticut.

Fire serving to release parts of a stand also promotes growth. This has been shown by Bruce and Bickford (1950) for longleaf pine; by Chapman (1941) who observed the combined effects of fire with seed years and a hurricane in the longleaf pine of Louisiana; by Wakeley and Muntz (1947) also for longleaf pine in central Louisiana; and Weaver (1947) for ponderosa pine.

Badoux (1946) examined 2126 pines in Switzerland and found that ordinary light thinning had only slight influence on current wood production. He stressed the importance of crown surface upon rate of growth.

Burns and Irwin (1942), working with pines in New England, observed that wide spacing increased the increment. Between the dry weight of foliage and the volume of 1940, and between the surface area of needles and the volume of 1940, they noted high correlation.

Jensen (1940), studying hardwoods in New England, reported that thinning in general helped growth but that growth increase declined rather rapidly after the second year. However, the factors in the response were very complex, and thinning changed the

relationships among air and soil temperature, evaporation, wind movement and humidity.

Ponderosa pines in Idaho were thinned by cutting (Miles, 1945) and showed an initial period of rapid growth followed by a decline of relatively short duration, and then a decided upturn. Are we able to distinguish such growth surges produced by thinning from those produced by other factors? In past times, as today, natural thinning occurred by disease, storm and other types of induced mortality. The problems thus brought up are amplified by Gevorkiantz and Olsen (1950) who, working on upland balsam fir in the Lake States, said that " Degree of competition does not remain the same even within a relatively short period of time, such as one decade, except in very old stands or in stands where the density is already near the assumed normal ".

Pearson (1943) reported on 15 to 30 years of observation of 8000 ponderosa pines in the Southwest. Although release stimulated growth, " the growth of individual trees is determined more by space available for root expansion than by crown size ". A large soil mass from which to draw moisture is of greater importance than leaf area. In fact, " a relatively small leaf area will suffice for the essential photosynthetic processes ". The work of Pearson in 1944, having to do with cutting cycles in ponderosa pine, brings forth the suggestion that surges, or cycles, of growth amounts by natural thinnings might in some respects simulate surges due to fluctuations of climatic factors. Such cycles suggest themselves also in the work of Roe (1947) with ponderosa pine in the Bitterroot region of the northern Rockies. After thinnings of various intensities, measurements made at five-year intervals for 35 years showed increased growth at the second, fourth and sixth lustrums. Rainfall, April–August, increased at the second and the sixth interval measurements but not at the fourth. To Roe it seemed that growth rates were influenced more by stocking of the stands than by variations in growing season rainfall.

The summary work of Pearson in 1950 carries even more emphasis on the recurring sequence: natural mortality, release of survivors and greater growth, adjustment and growth decline. As an epitome of this Pearson said that " there is a tendency for casualties to come in surges ". Can we as ecologists be certain that we can distinguish growth layers made by release surges from those

made by alternating series of wet and dry growing seasons? Students of climate must consider this intriguing idea, well known in forestry, when they interpret growth layers formed centuries in the past.

Zillgitt (1944), working with sugar maple in the upper Middle West, found that light cutting increased the rate of diameter growth, more so as the diameter of the original tree increased up to 18 inches diameter breast high. Above this size the rate was nearly constant. Furthermore, " the ratio of diameter growth at any given level to the growth at diameter breast high was equal to the ratio of the diameter at that point to diameter breast high ".

As we review the work of foresters and botanists we become more and more impressed with the wealth of information available to those of us working in tree growth.

DEFOLIATION, TOPPING, PRUNING. Defoliation, whether by natural or artificial means, affects tree growth in a fashion nearly opposite to that of thinning. Removal of a portion of the photosynthetic apparatus from a tree may be expected to reduce the amount of food manufactured and thereby the amount of xylem produced. In the southern Appalachians, Barrett and Downs (1943) pruned white pine in order to determine the growth response: " About 30 per cent of the number of living whorls may be pruned without seriously reducing the growth rate ". Boggess (1950) tried repeated prunings of planted slash pine in Alabama in order to determine the effect on diameter and height growth. The trees were pruned one-quarter, one-half and three-quarters of the way up the stem. Both height and diameter growth were correspondingly decreased. In fact, " any drastic reduction in the leaf surface of a tree will cause reduced growth. In forest stands reduced leaf surface may result from defoliation by fire, insects, disease, or pruning by man ".

Paul and Smith (1950), in their work on southern yellow pine, employed both cutting and pruning. Partial cutting often caused a sudden increase in ring width. Instances have been recorded where diameter growth of 80 years was doubled in 20 years of released growth. In contrast, severe pruning of the crowns caused a reduction in width of growth rings and curtailed spring-wood growth more than summer wood.

Pruning is of course artificial defoliation. Baker (1941) studied

gypsy moth defoliation in New England. *In general, defoliation preceded diameter decrease in the same years. The greater the degree of defoliation, the greater was the decrease.* In the words of Baker, " Growth and defoliation data of four species of oaks and white pine show a direct correlation between percentage of defoliation and decline in radial increment ". Over a ten-year period one-third of the diameter growth was lost. This becomes even more important when one learns that " Rainfall measurements taken at nearby weather stations indicated generally a lack of relation between variations in precipitation and growth rate ".

In his interesting work of 1949 Church discussed defoliation in a very thorough fashion. Whether defoliation is natural—by insects, fire, disease, storm or other causes—or is artificial, it always results in decreased diameter growth, an effect which can be spread over a large area. Less food materials are produced and hence less xylem is made. Church discussed six different insects whose attacks " under favorable conditions . . . can build up to epidemic proportions and sweep disastrously through millions of acres of valuable timber ". The decrease in growth commonly matches the amount of defoliation. On the whole, the effects of defoliation are so similar, regardless of the cause, and the positive and negative responses in wood production are so complex that it would be difficult indeed to pin down the specific cause for growth-layer variations in the past if one suspected defoliation of any kind.

It seems, however, that a ground fire which scorched entirely the crowns of shortleaf pines in the southern Appalachians (Jemison, 1943*b*) had no effect on diameter growth—it proceeded at a normal rate. In contrast, Stone (1942) sampled both burned and unburned longleaf pine in Mississippi and found a decided reduction in growth. Trees smaller than six inches diameter breast high averaged 23 per cent less growth during the year following the fire, whereas larger trees averaged 19 per cent less. Normal radial growth was usually resumed the second year after the fire.

Wagner in 1949 made an instructive study of the Coulter pine in southern California. Because of sudden cold, such as the drop in temperature in January, 1944, after 11 days of abnormally high temperature, or because of drought prolonged late into the autumn, the tops of the conifers were killed. Such dying at the top gave a narrow growth layer the succeeding year.

Reduction in growth due to pests of various kinds is recognized by Schulman (1945*b*, 1947). Not only may there be sharply reduced growth but also there may result a " complete quiescence of cambial cell division for one or more seasons " (1945*b*). Such a statement regarding cambial activity must surely be meant for a single inspected locality of a tree—it would seem difficult to prove for the entire volume of a tree, bole, branches and roots.

Defoliation caused by late frost, insects or droughts frequently produced double or triple false rings in hardwood trees which therefore were of little value to Weakley (1943) for chronology building. In particular, hackberry trees " go into temporary dormancy at almost any time during the growing season when the moisture supply becomes too scant to support further active growth. The result is almost invariably a false ring which frequently cannot be distinguished from a true annual one ". For his tree-ring record in western Nebraska, Weakley used red cedar and ponderosa pine, the cedar showing a greater tendency toward doubling than the pine. In contrast with the hardwoods, however, the double rings in cedar were diffuse and thus recognizable. One wonders, in view of the statements concerning double rings in hardwoods and softwoods, how certain Weakley was that no sharp double ring existed in the cedars or pines.

No better summary, perhaps, of the two opposites, release and defoliation, exists than that of Pearson (1950). Anything which interfered with the hydrostatic or photosynthetic systems reduced growth. Pearson listed rodents, insects, browsing animals, mistletoe and fungi. These damaging agents, 12 at least, reduced growth and made serious inroads on timber production in the Southwest. But it is in the fluctuations of growth, either by release or by defoliation, that our chief interest lies at present. These fluctuations may be local or widespread; they may be brief or prolonged. What, then, are the criteria by which such fluctuations can be distinguished from climatic effects? Sometimes the effects are quite similar, other times not (Sampson and Glock, 1942).

Various other factors have been described as influencing growth, but only a few can be mentioned here: the effect of insolation and exposure (Boyko, 1947); wind (Hopkins, 1939; Oosting, 1948); woodchuck droppings near trees (Wallihan, 1947); litter removal (Jemison, 1943*a*); and the combination of borer attacks and

drought (Secrest, MacAloney and Lorenz, 1941). Beal (1943) correlated tree growth with outbreaks of the Black Hills beetle and found that most outbreaks occurred during times of deficient precipitation. However, exceptions prove that " epidemics may also occur during years of ample rainfall when growth is favorable ". Loss of effective rainfall by interception (Hamilton and Rowe, 1950; Rowe and Hendrix, 1951) is difficult to evaluate where rain gauge records alone are available. According to Rowe and Hendrix, the average annual interception loss among second-growth ponderosa pine in California was 12 per cent. Throughfall, stem flow and interception loss were directly related to storm size.

ABNORMAL VERSUS NORMAL SITES. Curiously enough, two workers apparently insist upon using abnormal trees from abnormal sites, whereas botanists and foresters attempt to use normal trees from normal sites or else select trees in order to compare the effects of different sites. The first group seeks to reproduce a meteorological, or runoff, record of the past, whereas the second group seeks to understand the details of tree growth and its response to the various interacting factors of the environment.

Douglass (1941, 1942, 1945, 1946a, b) and Schulman (1942a, 1943, 1945a, b, 1947, 1951, 1951–52a) have repeatedly emphasized that accurate climatic (rainfall) records can be found only in abnormal trees from abnormal sites. Steep rocky slopes, with soil present in patches or in crevices, at the lower forest border in the Southwest give them trees with ideal climatic records. In 1948, Antevs had apparently come to approve the use of abnormal material. A knowledge of soil, soil moisture, groundwater and topography perhaps militates against the use of trees from abnormal sites. Douglass (1941, 1942) described Douglas-fir growing on the precipitous slopes of canyons in Mesa Verde National Park and said (1942) that the trees are thus compelled " to subsist on the precipitation that falls on their own area ". Such trees can record rainfall of their immediate area only if the runoff downslope to the trees equals the runoff downslope away from the trees. If the trees give a record of rainfall, they do so in spite of the steep slope, not because of it. Because the principles underlying the relation of topography to groundwater penetration and its subsequent percolation are much the same over the face of the earth, it is of interest to read that " people who live in moist climates have great difficulty in

judging these topographic characters " (Douglass, 1941) ; or that specimens should be taken " in the field by someone who understands the effects of topography " (Douglass, 1941). Surely plant ecologists and geologists understand the effects of topography, and in addition they realize vividly that the amount of water penetrating the soil on a steep slope or the soil in pockets does not necessarily represent accurately the amount of rain falling on a particular part of the slope. On a steep slope runoff may not only bring water to a tree, but may also carry it away. Douglass said (1946a) that trees growing on high isolated points or in a crack in a rock are thoroughly protected from any imported water. True ; but they are not protected from water exported before they have a chance to use it.

Schulman likewise emphasized selection of trees from adverse sites. Very dry sites in the Rocky Mountain region are " often characterized by open and scraggly but over-age stands " (1943). Great longevity accompanies great hardship. Samples are preferred from a tree growing " on a rocky southeast-facing lower slope of some 30° or less " (1943) ; or from a " steep open site . . . on a dry ridge-back ".

In the Pacific Northwest, " Trees were selected (for core samples) on steep slopes and ridges bordering the coulee floors and at the dry lower forest limit " (Schulman, 1945a).

Single cores were taken from ponderosa pine and Douglas-fir scattered over the Colorado River basin (Schulman, 1945b) : ". . . all sites represent well-drained slopes or ridges with thin soils and are near or at the lower forest border, where drought stresses are important ". No wonder the trees " eke out a precarious livelihood ". This being true, it is a bit difficult to agree that " The general advantage of marginal regions as source areas for dendrochronologic material seems obvious ". Douglas-fir, a dry-site, slow-growing type, is said to be the best tree for chronologic purposes. Its normal site is on steep dry slopes. This must be compared to the statement of Preston (1940), the forester, wherein he says the Douglas-fir is " adapted to variety of soils but best on moist, deep, porous soils of northern exposure ; will endure considerable drought . . .". Or again we should refer to the statements of Harlow and Harrar in their Textbook of Dendrology (1950) : " Trees are found on a variety of soils but make their best

growth on deep, rich, well-drained porous loams in regions where there is an abundance of both soil and atmospheric moisture. . . . While [the Rocky Mountain form] most abundant on moist sites, it is quite drought-resistant and is often found on arid areas with ponderosa pine ". It seems to be true that Schulman prefers dwarfed trees or those with "branching snag tops ". In fact, the frontispiece of the publication (1945b) shows an isolated 15-foot Douglas-fir with a snag top and at least 60 per cent of the branches dead. These abnormal trees growing in the inhospitable environment of " upper steep and rocky slopes ", where one would expect a minimum of soil moisture retention and a maximum of exported water, are said to give a record of the previous winter, October–June, rainfall. Therefore, " Logic suggests and experience has proved that the best drought-sensitive ring records come from upper, steep, and rocky slopes ". With this emphasis on drought effects and lack of soil moisture at abnormal lower forest border sites, we must of course agree.

In southern California, " Only trees on dry, rocky slopes or ridges were selected for sampling; all sites were on the predominating granite " (Schulman, 1947). Adverse sites where growth is slow and highly variable are most fortunately located to yield trees for chronology (Schulman, 1951).

In the Big Bend National Park of Texas, cores were taken from a " sparse stand of Douglas-firs, stunted, slow-growing, and seldom reaching 20 inches in stem diameter ", and "truly of an outlier character " (Schulman, 1951–52a). Nineteen cores, taken from Douglas-firs, represented almost all the mature trees of the area.

In the Ouachita National Forest of Arkansas, Schulman (1942a) took six cores from shortleaf pine which were " scattered over a well-drained secondary ridge top " at an elevation of 1300 feet. Three cores were from pines on a site with poor drainage which " would be considered an unsatisfactory source of specimens for climatic study in dry climates ". These specimens showed sequences of growth layers that were " erratic and lacking in sensitivity ". Turner (1936b, 1937), who also worked with the pines of the mountain areas of Arkansas, studied them in relation to soil and topography. On the steeper slopes, he said, stony areas and exposed rock were common. These situations obviously belonged to what Turner called inferior sites in contrast with in-

termediate and superior sites: " Sites with lower site indices are on soils with a high degree of slope and hence excessive water run-off, or extremely stony, or gravelly, or sandy soils with moderate or steep slope . . .". The poorest pine sites in Arkansas were on mountain soils where the slopes were excessive or where soils were gravelly or stony (Turner, 1937). Giddings (1941), who worked in central Alaska, sampled trees from sites which he described as " rocky faces of steep bluffs ", or again, " stocky, rather stunted, and malformed spruces rooted in thin, rocky soil high on a steep north slope ". However, he also took samples from trees which grew on lower slopes, river bottoms, and along river banks. It is of interest to note that he found different sequences of rings on different sites.

Smiley (1951) subscribed to the selection of trees apparently from abnormal sites, and it is of interest to botanists and ecologists to read that " Trees, in order to produce a climatic record, must grow under special conditions such as on a steep slope where ground water is present only after precipitation; they must have a definite growing season and react favorably to one controlling climatic factor ". What is the significance of the phrase, " react favorably to one controlling factor "? In the Southwest, Smiley said that members of the Pinaceae " give the best climatic records where they are found growing under severe conditions rather than under optimum ones. The forest border, where the forest thins out and stops (because of a climatic change) as the elevation decreases, normally has excellent climatic records present ". Thus, in summary, Smiley believes that trees give the best climatic records where located on steep slopes under severe conditions at the very edge of the lower forest border zone.

Weakley (1943), who worked in western Nebraska, selected his trees carefully and found that those " which grew on hillsides or on benches well above dry washes are most affected by moisture fluctuations and generally are usable ". On the one hand, trees " which grew wherever run-off or stored moisture increased the supply received by direct rainfall were not so responsive to yearly fluctuations of rainfall and consequently are of little or no value ". There is no word about runoff causing a decrease in the supply of water. On the other hand, " trees which have been in very exposed and difficult positions such as high south slopes or the tops of narrow sharp ridges generally have such compressed and distorted

rings that they too are of little or no value ". These statements involve a nice sense of judgment of the correct amount of water to give a climatic record by inspection of the rings so produced. These clear statements by Weakley concerning the selection of trees in western Nebraska should also be contrasted with the somewhat more extreme statements concerning selection of trees under even more rigorous conditions in the Southwest.

Will (1946) worked on trees near Bismarck, North Dakota. His search was " confined to the sides of the many coulees leading down from the bluffs to the lowlands ". Finally he found a burr oak growing on colluvial material whose slope upward from the oak was 35°. The construction of chronologies and their use as climatic records in western Nebraska and central North Dakota should perhaps take into account the work of Wiggin and Verduin (1946–47) who found that two annual rings were rather common for 1946 in southeastern South Dakota. In addition, multiple growth layers were far from rare on the High Plains of Texas (Glock, 1951).

Biologists and others have been guided apparently by their desire to study sites normal to a region and the effect of such sites on normal tree growth. Dale (1947), writing about drought in the Great Plains area, said that " it isn't the amount of water that falls which counts. The important thing is the amount of water that soaks into the ground and is kept there until crops can use it ". With trees it would be the same, and the role of steep rocky slopes in view of what Dale said is obvious.

Many years ago Kapteyn (1914) held that trees should be taken from uniform conditions, with good subsoil water. He selected oaks from along the Main, Moselle and Rhine Rivers, and measured their rings. The results obtained appear to bear out the wisdom of his selections.

Recently Tarrant (1950) studied the relation of topography to site quality for Douglas-fir. The better sites are the concave lower slopes and depressions, whereas the poorer sites are the convex upper slopes, ridges and hilltops. In New England, Burns and Irwin (1942) measured amount of wood production as an indication of needle efficiency in white and red pine. They used trees in plantations on level land with porous homogeneous soil and no runoff.

In 1941, Friesner and Friesner compared rainfall to the growth

of trees from " sites subject, because of topography, to minimum amounts of run-off " (Friesner, 1950). In 1950 Friesner carried his work further in order to " determine the possible effect of a site where run-off, because of steep slopes, is certain to be high ". Agreement between tree growth and rainfall decreased notably on the steep slopes.

Giddings (1941), as before mentioned, did not confine his collections to trees growing on adverse sites but took them from river bank upward to timberline.

In north-central New Mexico Glock (1950) collected samples from trees which were growing in the upper part of the Transition Zone and lower part of the Canadian: ". . . the locations were chosen so that abnormal drainage toward or away from the trees was at a minimum ".

Gladwin (1940*b*) attempted to choose his trees " so as to give the widest range of environment within the area "; hence some trees were chosen from level ground and probably deep soil, others from steep slopes and probably shallow soil.

Hansen (1938) studied ring growth and the reproduction cycle in Engelmann spruce from near upper timberline in the Snowy Range of southeastern Wyoming. Although he took samples of trees on level surfaces or gentle slopes, the conditions were unfavorable because of thin quartzose soils, strong winds and low temperature. Hansen later (1941) studied ring growth in central Washington near the lower forest border. The collecting area lay on a sharp slope with shallow sandy soil. At places bedrock was exposed at the surface. Runoff is high during heavy rains and during the winter when the ground is frozen, which is important in view of the fact that less than 30 per cent of the mean annual precipitation falls during the growing months. The " physical factors of the environment are neither at an optimum nor in adjustment with one another ". Because of low summer rainfall and high temperature, growth is not normal, according to Hansen.

Hustich (1948*a*) worked near the northern limit of tree growth in Finland and his trees were situated " on dry moors in river valleys where drainage is sufficient ".

Lyon (1943, 1949), working in New England, selected trees from a variety of slopes and soil depths, and from upland and bogs. Even in humid New England, Lyon has emphasized, conifers

show " the dominance of the water supply factor in determining the relative width of the annual ring . . ." (1943). This contrasts rather startlingly with the insistence of workers in the Southwest that only trees growing under near-desert conditions with soil moisture in short supply yield a record of rainfall. Lyon said: " For hemlock and white pine, the correlations between relative growth rates and the precipitation records of certain periods of the year are so high that the occurrence of a notably narrow or wide ring of wood is presumptive evidence for a drouth or a generous supply of water to the tree for the growing season in which it was formed ".

Paul and Smith (1950) pointed out that on steep slopes most of the precipitation runs away on the surface and therefore is not available to the roots of trees. Such a condition could stop growth during a season. In Indiana Reimer (1949) studied the growth of deciduous trees which grew on rather level land with fair to good drainage. Storie and Wieslander (1948) studied timber sites in relation to soils in California. The best sites were well drained, whereas the lower quality sites had either poor drainage or excessive runoff.

In summary, it is clear that recent studies emphasize three things: a) local site factors down to those at a single tree are of great importance in tree growth; b) local site factors are an interacting complex; and c) most students try to study normal trees growing under conditions normal to an area. The importance of local site factors, even around the single tree, was well emphasized by Gladwin (1940b). Among those who point out the complexity rather than the simplicity of site factors, attention may be directed to Briegleb (1945), Friesner (1943b), Gladwin (1940b), Huber (1948), Kienholz (1934-35), Moseley (1941), Shirley (1945), Tihomirov (1940) and Zeuner (1951a).

ANATOMICAL STUDIES

Little can be done intelligently with growth as a basis of interpretation until something is known concerning growth itself. Hence botanists have bent their prime efforts toward the ecology, physiology and anatomy of growth. Such growth applies to all parts of the plant body, to the entire stem and to the roots, to elongation and to diameter increase.

HEIGHT GROWTH OR ELONGATION.   It would be impractical to summarize all work on this important topic.   The material to which reference is made constitutes, it is hoped, a cross section of the chief trends of investigation having to do with the topic in hand.

The times of beginning and ending of elongation are spread over a considerable interval, depending, somewhat but not wholly, upon species and upon latitude or altitude for a particular longitude (Byram and Doolittle, 1950; Cook, 1940; Daubenmire, 1950–51; Friesner, 1942a, 1943a, b; Johnston, 1941; Kienholz, 1934–35, 1941; Pearson, 1950).   In the case of growth initiation the time spread is less than that of growth cessation.   Many species show the grand-period type of elongation behavior with the maximum rate-point spread over a time interval, whereas other species show a marked modification of the grand-period type of growth curve (Friesner, 1942a, 1943b).   Some species begin growth early and stop early, others begin early and stop much later, and others begin late and stop early (Cook, 1940; Friesner, 1942a; Johnston, 1941; Kienholz, 1934–35, 1941).   Friesner (1943a) learned interesting facts from a comparative study of elongation in primary, secondary and tertiary axes of two species of pine in Indiana.   In general, the primary axes grew at a greater rate for a longer time than the secondary, and the secondary at a greater rate for a longer time than the tertiary.   The outer or upper secondaries, however, elongated over a longer interval of time than those lower on the tree.   For a period of more than two years the writer measured tip growth of trees in Maryland which grew within 20 feet of each other on a lawn.   The time of growth initiation for all branches was spread over a very short interval.   In contrast growth cessation varied all the way from early June to late September, not only among the trees but among branches of the same tree.   It is clear, therefore, that the varying and variable time limits of the growing season for elongation provide a rather complex problem in the correlation of growth with one or more of the ecologic factors.

The time of extension and the time of radial growth do not by any means coincide.   In India Chowdhury and Tandan (1950), working with broadleaved trees, found that the gap between extension and radial growth varied from two weeks to three months. This, they said, differs from Europe and North America where the

two activities begin at the same time. Such coincidence, however, is not exact. Kienholz (1934–35) found considerable variation among conifers in New England. With the orange tree Reed and MacDougal (1937–38) found that shoot growth preceded cambial activity by more than a month. Reimer (1949) worked with five species of deciduous trees in Indiana. All five exhibited the grand-period type of growth and belonged to the short-period type of axial extension. As regards axial elongation and radial enlargement, " It is rather well defined that these two types of growth are alternate ". This is shown by the following dates: *Prunus*, April 14–June 4 (axial), May 26–September 30 (radial); *Acer platanoides*, April 7–May 26, June 17–August 4; *A. saccharum*, April 14–May 26, June 10–August 25; *Tilia*, April 21–June 17, June 17–September 22; and *Fagus*, April 7–May 26, May 19–August 25. In general, Reimer says, axial growth is more likely to precede radial growth in deciduous trees than in conifers where the reverse may be true. Hustich (1945), working in North Europe, noted little quantitative correlation between length growth and radial growth of the same year; however, it was much higher with the previous year. Volume growth correlated very well with lengthening.

Many attempts have been made to correlate height growth with one or more of the meteorological factors which could conceivably influence growth at a particular time. Some attempts (Aaron, 1948; Craighead, 1941; Fowells and Kirk, 1945; Friesner, 1943a; Hustich, 1945; Kienholz, 1934–35; Pearson, 1950) have apparently yielded favorable results, others not so favorable (Cook, 1940, 1941a; Johnston, 1941), and still others a mixed reaction or a dependence upon other factors (Friesner, 1943b; Hustich, 1948a; Pruitt, 1947; Turner, 1936b). According to Cook (1940, 1941a), terminal growth has little relation to current temperature or rainfall in the Northeast; it is, instead, of a generic character. Fowells and Kirk (1945) found that height growth of ponderosa pine seedlings " was about proportional to the amount of soil moisture available and to the amount of water transpired ". In Indiana Friesner (1943a, b) found a mixed reaction: the type of growth curve in some species was little modified by external conditions, in others it was seemingly in agreement with temperature. The start of bud activity (1943b) depended upon environmental factors,

the most important being temperature; or (1943a) the start of elongation in pine depended upon growth substances released or elaborated by terminal buds. Hustich (1945) obtained rather high correlation between length growth and temperature of the previous year but only slight correlation between length growth and July temperature of the current year. A high temperature one year in North Europe gave long shoots the next year (1948a). Years of maximum flowering intensity in pine commonly coincided with years of long shoots (1948a). In New Hampshire, Kienholz (1934–35) studied leader elongation of pine. Growth did not correlate with daytime temperatures; however, it had a high correlation with minimum night temperatures and with mean night temperatures. Pearson (1950), working in northern Arizona, found that shoot growth during the early part of the season was a sensitive indication of temperature, whereas later soil moisture gained control. In fact, shoots attain greater length when April-May receive above average rainfall. Pruitt (1947), working in the Southeast, determined that a definite correlation existed between height growth and the relative position of the water table. From his observations in Arkansas, Turner (1936b) learned that rather high correlation existed between rate of height growth and soil series type. Much work remains to be done upon the factors which initiate elongation, guide it and stop it.

Uncertain as we may be concerning the strict conformity of elongation to climatic factors or the exact effect of growth-promoting substances, we may nevertheless reasonably expect to find evidence of growth fluctuations, even during the regular growing season, because of temperature and rainfall variations. Friesner (1942a, 1943b) noted elongation in Indiana both before and after what he called a mid-summer zero point. Such double waves of activity have been rather commonly noted; for instance, by Byram and Doolittle (1950) in shortleaf pine in the South, by Chowdhury and Tandan (1950) in broadleaved trees in India, by Friesner (1943a), by Kienholz among conifers (1934–35) in New Hampshire and among hardwoods (1941) in Connecticut, and by Reimer (1949) among hardwoods in Indiana. More than this, Friesner (1943a) detected " three waves of intensity " on the primary axis of *Pinus strobus* and *Pinus resinosa*. The writer measured tip growth for two years on a peach tree in Maryland and recorded a

mixture of two and three waves of activity per season. One branch with three tip increments in one season showed two distinct zones of terminal budscale scars within growth for that year. In addition, he has noted multiple tip flushes in West Virginia, Maryland, Texas, Arizona, and in the Sierra Nevada of California.

Waves of activity in terminal growth do not seem at all unusual during what is commonly called the growing season. More and more such fluctuations are being recognized by daily observation and measurement. There is some reason to believe that waves of activity occur nearly the year around, even during the winter or dormant season, though of course at a low level of intensity. This varies somewhat from the thought of Maximov (1930) who said that growth does not take place during dormancy, even though " external conditions may be quite favorable ". So-called post-seasonal growth (Reimer 1949) could occur at any time after the mid-summer zero point of elongation or after the end of the grand period of growth, if such occurred, and before the rapid growth of the succeeding year. Spurts of post-seasonal growth following inactivity (after " plateaus " when periodic measurements of tip growth are plotted) and occurring within a growing season belong properly to that season; they may give multiple increments of tip growth. Here for the moment post-seasonal growth will refer to growth during late autumn and winter when dormancy occurs. Such elongation takes place either as true axial extension or as bud lengthening. Bell (1940) reported slow growth in length of the vegetative bud of the apple throughout the winter months in Nova Scotia. Activity in the bud, including differentiation and actual lengthening, have been noted by Friesner (1942a), Hustich (1948a) in Finland, Kienholz (1941) in Connecticut, and Reimer (1949) in Indiana. However, a slight amount of true axial elongation does occur (Friesner 1942a; Kienholz, 1941; Reimer, 1949). Evidence of bud elongation as well as of true axial lengthening has been gathered by the writer in Texas.

DIAMETER GROWTH. From an ecologic standpoint, growth layers give a more satisfactory record than do increments of elongation because growth layers are more sharply delimited and because they are more permanent. Several studies of the past decade bear directly upon the gross anatomy of growth layers, although no doubt much work remains to be done.

Inspection of a growth layer over its entire areal extent in a stem requires complete dissection of the tree. However, the differences found in different parts of the trunk as well as the unknown occurrence of partial growth layers makes dissection a requisite to complete knowledge of growth-layer distribution. Brown (1912) noted that the width of a complete ring decreased from apex to base in *Pinus rigida* from New York state. In New England, Burns and Irwin (1942) sectioned more than a score of red and white pines and found that the increment for 1940 had its maximum thickness at heights of 17 to 19½ feet in trees 20 to 24 feet high. They did not use increment borings because " the width of an annual ring at any level is not directly proportional to the annual increment's total volume ". Growth-layer thicknesses are taken on a linear basis, whereas total growth occurs on a volume basis. In contrast to the foregoing, Paul and Smith (1950) studied 75 southern yellow pines and found that wider growth rings were more prevalent in the lower than in the upper part of a tree.

In the Southwest, Krauch (1949*a*) examined the growth of Douglas-fir in relation to age. Best diameter growth occurred during the mature stage after the tree reached 240 years. Later, diameter growth decreased, although growth in the basal area continued at a high rate with a maximum occurring at age 340. Marr (1948), in his enlightening work near the forest limit east of Hudson Bay, found excellent circuit and longitudinal uniformity in relative thicknesses which asymmetry of trunk did not alter. An extreme case of asymmetry caused by the wind has been cited by Oosting (1948) in connection with a Monterey cypress from California collected by W. S. Cooper. The windward side contained 50 growth rings, whereas the leeward had 304.

Church (1949) has brought together a mass of information from the literature on the effects of defoliation by various agents on the growth of certain conifers. Because of the importance to growth-ring studies, the summary by Church cannot be passed over. Defoliation of spruce and balsam fir by the spruce budworm caused different degrees of retardation of growth in different parts of the crown: severe reduction in the top of tree, no change in the middle, and a decided increase near the base. When the budworms stopped feeding, a second depression of growth might occur because of heavy production of cones. Severe feeding could cause total sup-

pression of rings on parts of the trunk, although the spruce that recovered " showed no indication of missing growth rings ". The first result of defoliation of tamarack by the larch saw fly appeared as an absence of thickened tracheids in the autumn wood. Subsequently there was a reduction in the thickness of growth layers and in some cases an absence of growth in the base of the tree. A growth layer, however, was formed in the crown during every year until death. Defoliation by fire resembled that by insects in as much as reduction of growth took place for the most part in the lower portion of the tree. Defoliation by hail storm also retarded growth. Such a storm defoliated a young longleaf pine at the end of April, 1937, after most of the spring wood had been formed. As a result, only a narrow band of summer wood was formed, a circumstance of note when it is recalled that thin summer wood has also been ascribed to drought. The spring wood of 1938 was much less than normal and the summer wood exceeded it in thickness. In 1939 growth was still much below normal. Artificial defoliation indicated that gradual reduction in increment occurred after partial defoliation or after early spring defoliation of new growth among certain conifers. Late spring defoliation of new growth in jack pine gave greater reduction of wood in the top of the tree and killed it the second season. In contrast, early removal of old foliage gave decided reduction of ring thickness at the base of trees in years of defoliation. In summary, Church said that the degree of defoliation determined the amount of reduction in growth, that the reduction in diameter growth did not take place at uniform rate throughout the stem, and that in most cases the greatest reduction took place in the basal part of the tree.

Thus it appears that under both normal and abnormal conditions diameter increases vary within the stem of a tree. Such variations must be considered where growth-layer thicknesses are used as a straightforward measure of some one ecologic factor.

Studies made on portions of a growth layer, either the light- or densewood, have given somewhat diverse results. Church (1949) reported the formation of a narrow band of summerwood because of defoliation; Marts (1949, 1950) and Paul (1946) used pruning to decrease the springwood and thereby increase the percentage of summerwood; Paul (1944, 1946) and Paul and Smith (1950)

noted that a lack of summerwood was due to a deficiency of soil moisture during the growing season; and Schulman (1942*a*) correlated summer rainfall with summerwood formation. In the South, Paul and Smith (1950) and Schulman (1942*a*) found little variation in thickness of springwood; variations in summerwood responded to summer rainfall. Douglass (1946*a*) did not mention the possible cause of thin or weak late woods. To him a thin latewood following a wide earlywood signified a double or intra-annual ring.

It is clear that experimental work on the gross constituents of growth layers, such as was done by Marts, and Paul and Smith, are highly desirable in addition to the painstaking statistical work of Schulman and others. The matter, however, may be carried further, into detailed anatomical studies.

In eucalyptus, Amos, Bisset and Dadswell (1950) found the shortest fibers in earlywood and the longest in latewood, the change occurring suddenly. They established " an intrinsic relationship between growth rate and fibre dimensions ". Bisset, Dadswell and Amos (1950) extended the foregoing results by pointing out that variations in fiber length followed a characteristic pattern throughout the growth rings of trees in temperate climates. In New Guinea, where definite growth rings were absent, " there was no significant fibre-length variations in the wood laid down over several years ". In fact, " there must be a close relationship between cell dimensions and growing conditions ". Johnson (1942) worked with three species of *Populus* in Canada and found that fibers in fast-growing annual rings were longer on the average than those in slow-growing rings from the same tree. In single rings, fibers of earlywood were shorter and thicker than those of latewood. This evidence appears to be conflicting if earlywood grows faster than latewood. Wardrop (1951) related tracheid length to growing conditions, age and rate of division of cambial initials, and applied the information to growth of trees for lumber. If certain trees of the same species in the same group possessed longer tracheids in the first growth layer, then subsequent growth layers also had long tracheids. Thus nursery stock for strong lumber could be selected. Church (1949) noted that the first result of defoliation was the absence of thickened tracheids in autumn wood. Total vessel length in ring-porous and diffuse-porous hard-

woods was studied by Greenidge (1952). In the more highly specialized ring-porous woods vessels might extend the full length of the stem, whereas cross walls restricted the length of vessels in diffuse-porous woods. Therefore the " vertical rates of water conduction in large woody stems may be closely correlated with total vessel length ". A study of gymnospermous woods as well as the hardwoods suggested to Greenidge " that due regard should be given to the patterns of moisture retention in addition to moisture movement in any study of the water economy of a species ", a suggestion of value for the understanding of the fundamental relation between growth and climate.

One more point should be mentioned—the work of Amos, Bisset and Dadswell (1950) on eucalyptus. Early in the 1944–1945 growing season the water balance was overtaxed, as shown by a saturation deficit and temperature higher than normal and a rainfall lower than normal. This produced a type of anomalous tissue near the start of the growth layer which resembled somewhat the frost injuries described by Glock (1951). In the one case the injury was due to drought, in the other to frost.

MULTIPLE GROWTH LAYERS. The problem of multiple growth layers in a single year is a difficult one, and its proper solution bears directly upon the validity of much tree-ring work. Such difficulty is highly important because so much of current work uses trees grown under the variable ecologic conditions of forest zones adjacent to the arid regions. It is self-evident that a study of cambial activity is fundamental to an understanding of its periodicity, whether intra- or inter-seasonal.

Among those who have detected a single period of cambial activity are Byram and Doolittle (1950) in the shortleaf pine of the South, Friesner (1941) in the beech of Indiana, Friesner and Walden (1946) in *Pinus strobus* of Maine, and Chowdhury (1940) in three species of diffuse-porous wood in India. Friesner and Walden contrasted their results with those of Brown (1915) who found two periodic optima of growth in *Pinus strobus* of central New York, one during May and early June, and the other in July and August. Other students, concentrating on the growth layers themselves, have observed doubles absent or rare: Hustich (1948*b*, 1949), among conifers at the polar border in Finland; Marr (1948), among conifers at the polar border on the east coast

of Hudson Bay; Moseley (1941), among hardwoods of the Northern States; and Will (1946), in an oak near Bismarck, North Dakota.

In the detailed work of Hustich (1949) and Marr (1948) close observation and careful statement provide convincing argument for the unity of the annual increments.   In contrast, Moseley (1941) stated: " In the Northern States I have never found a hardwood tree of any kind . . . that formed two rings in one year ". The statement might be regarded as rather broad.   In North Dakota, Will (1946) did not expect trouble from double rings because " the season is generally too short to allow the double ring formation ".

Questions raised and observations made by Brown in 1912 carried highly suggestive ideas for students of tree growth.   Double rings, he found, were common in New York and " might easily cause miscalculation as to age ".   In broadleaved trees doubles were ascribed sometimes to defoliation and at other times to favorable and unfavorable external factors.   In *Pinus rigida* double rings must have been caused by external factors.

Among those who have detected multiple periods of cambial activity within a season are Chowdhury (1940), in one species of ring-porous wood from India; Daubenmire and Deters (1947–48), among deciduous and evergreen trees in the summer-dry climate of Idaho; Friesner (1942*b*), in two species of broadleaf trees in Indiana; Kienholz (1934–35), in red pine of New Hampshire; and Reimer (1949), in four out of five deciduous species in Indiana.

Double rings whose presence has been determined by the growth layers themselves have been noted by Dobbs (1942) in England; by Glock (1951) among many species in West Texas; by Senter (1938) especially among oaks of the Middle West; by Weakley (1943) among red cedar and ponderosa pine of western Nebraska; by Wiggin and Verduin (1946–47) among nine species of hardwoods in South Dakota; by Schulman (1940*c*) along the California coast, the Pacific Northwest (1945*a*), in Southern California (1947), in South Texas (1951–52*a*), and in Arkansas (1942*a*); and by Douglass (1946*a*), Gladwin (1940*b*), Hawley (1939, 1941) and Schulman (1941, 1945*b*, 1951) in the Southwest.   If one interprets their explanations correctly, he concludes that Douglass, Gladwin, Hawley, Schulman and Weakley feel rather confident of

their ability to detect false rings by their fuzzy outer borders, by their positions within the annual increment or by crossdating. The relation of double rings to crossdating will be discussed later.

Several of the above studies call for special remarks.

In Idaho Daubenmire and Deters (1947–48) observed growth slow-down in mid-season due to low temperature. As a matter of fact, growth rate as measured by dendrometers varied from slowing down to actual shrinkage. This basic work of Daubenmire and Deters is highly suggestive as regards an ultimate understanding of cambial activity and the course of growth. Reimer (1949), using dendrometers on deciduous trees in Indiana, observed two peaks of growth in *Prunus,* two peaks in two species of *Acer,* and three peaks in two species of *Fagus.*

Douglass (1946*a*) and Schulman (1951–52*a*) suggested that proper illumination and a surface cut diagonal to the grain give the best means of distinguishing annual from non-annual rings. In addition, Douglass said that a double ring in the Southwest commonly has the following sequence: wide earlywood, faint latewood, narrow earlywood, and heavy latewood. This was true especially if the faint latewood was hazy. However, Church (1949) recorded the same sequence as comprising two annual rings, the faint summer wood having been caused by a storm which defoliated the tree. If the faint band of latewood occurred close outside (toward the bark) the heavy band of latewood, according to Douglass, the sequence comprised two annual rings. The writer, however, has observed hundreds of cases of faint densewood bands just outside heavy bands in West Texas, and all of the heavy bands were part of an intra-annual (Glock, 1951).

Douglass (1946*a*), Gladwin (1940*b*), Hawley (1941) and Schulman (1941, 1945*b*, 1951) in the last analysis have claimed a solution of the difficulties inherent in double rings by means of crossdating. In this connection Schulman (1945*b*) has aptly remarked that " at the lower forest border . . . false rings tend to appear at times indistinguishable from true annuals ". He found the same to be true in California (1940*c*). As a summary he wrote (1941) : " There exists a complete array of types of false annual rings ranging from those which are extremely ill-defined to those which cannot be differentiated from true annual rings until they are cross-dated ". And a step farther was taken by Douglass

(1946*a*) : " Crossdating . . . put exactness into the dating of tree rings . . . the feeling of precision in our chronology building has grown stronger and stronger . . . . We were fortunate . . . in having a large climatically homogeneous area . . .". In view of the above quotations it is highly pertinent to refer to the work of Dobbs (1942) who studied over 100 sections of larch that came from an area of 50 mile radius around Bristol, England. Double rings were so common that Dobbs used them for crossdating purposes : " there was a general and recognizable pattern formed by the false rings ". Therefore, if intra-annuals exist which are indistinguishable from true annuals, and which occur in areas climatically homogeneous, it is difficult to see how crossdating alone can reveal their intra-annual character.

A final point in connection with double rings must be mentioned. Weakley (1943) in western Nebraska and Wiggin and Verduin (1946–47) in southeastern South Dakota had difficulties with double rings, and Weakley even with triples, whereas Will (1946) had no such difficulty in south-central North Dakota. He said : " In this northern region that difficulty seems to be very slight as the season is generally too short to allow the double ring formation ". It has been recorded, of course, that Friesner and Walden (1946) found only one peak of growth per season, that Marr (1948) gave strong evidence for unity of the annual increment in trees on the east coast of Hudson Bay, and that Moseley (1941) had never found a double in the northern States. In addition, it has been recorded that Brown (1912, 1915) detected double rings prevalent in central New York, that Kienholz (1934–35) found two peaks of growth in New Hampshire, and that Friesner (1942*b*) traced two peaks of growth in Indiana. Somewhere between the polar border of the forest, as recorded by Marr and by Hustich (1949), and South Dakota, New York and New Hampshire the single annual increment of the north gives way to the double tendency of the south; *it* would be most interesting indeed *if the* transition occurred between North and South Dakota. However, we shall await more evidence. Schulman has said (1945*b*) : " It has been observed by Douglass that in the Southwest ring duplicity (*sic*) in this species (*Ponderosa pine*) was of increasingly frequent occurrence with decreasing latitude ". Is the problem so simple ?

ROOT GROWTH. In Pennsylvania, Wood (1934) studied roots because, as he said, " so little is known of the root systems of forest trees larger than seedlings and because most of the major problems of silvicultural practice in the forests of the eastern United States are linked in some way with roots ". The roots of a chestnut oak comprised 45 per cent and the trunk and branches 51 per cent of the total weight of the tree; the crown spread covered 22 square feet, and the root spread, 229 feet. Undoubtedly the root system makes up an important part of a tree. In her study of grass roots in Rhode Island, Stuckey (1941) wrote that: " Root growth and its influence on the subsequent development of the plant has always been recognized as important in respect to food and water relationships . . .".

The growth of roots occurred in two spurts during a growing season, as shown by the work of Harris (1926) with apple and filbert roots, of Kaufman (1945) with jack pine in Minnesota, of Kienholz (1934–35) with certain conifers in New Hampshire, of Pessin (1939) with longleaf pine and associated species in southern Louisiana and Mississippi, of Preston (1942) with lodgepole pine, of Stuckey (1941) with grasses in Rhode Island, and of Turner (1936a) with two species of pine. Harris and Turner ascribed the mid-season resting period to lack of soil moisture. In Minnesota, Kaufman ascribed reduction of rate of root growth to a drop of available moisture to less than four per cent and a high rate of evaporation. Morrow (1950) observed the growth of roots of sugar maple throughout a mild winter in central New York. Early autumn drought stopped root growth. He asserted that: " Shoot growth, cambial activity, leaf activity, and root growth demonstrated no correlation, except that the maximum growth of each occurred during the same period of the year ". Stuckey noted that cell division in root tips occurred at temperatures very close to 32° F. and took place slowly all winter.

To some it may be new to learn that root systems are in the main surprisingly shallow. This has been shown by Le Barron (1945) with black spruce in Minnesota, by MacAloney (1944) with jack pine, by Pessin (1939) with longleaf pine and associated species in southern Louisiana and southern Mississippi, by Preston (1942) with lodgepole pine, and by Scully (1941–42) with hardwoods in Wisconsin. Bannan (1941–42) found that the lateral roots of

Thuja were no deeper than six inches and most of them only two or three inches deep. Le Barron observed that spruce in northern Minnesota had a shallow spreading root system, no matter whether the soil was well or poorly drained. In southern Louisiana and Mississippi, Pessin found most lateral roots in the upper one foot of soil. Under normal rainfall pine seedlings and associated plants obtained plenty of soil moisture, but during drought the trees suffered because grasses took so much of it. Preston found the majority of roots of trees one to 15 years old in the upper six inches of soil, and a tendency to increase the average depth with age. The lateral roots of greatest length were almost invariably shallow. Roughly speaking, Scully found that the upper eight inches of soil contained 80 per cent or more of the total root volume.

Bannan (1941), working with the variability of wood structure among the roots of eight species of conifers native to Ontario, chose his materials from different habitats and from different parts of the root systems. The proportions of early- and latewood, the size of tracheids and the thickness of their walls varied greatly in different parts of the root system and in different specimens. No consistent relationship existed between soil moisture and tracheid size; there was much dissimilarity between trees of the same species growing under like soil conditions, and sometimes the same diverse tendencies between roots of the same tree. More such work on anatomy, or ecologic anatomy as it were, is highly desirable.

The writer does not presume to be able to select all important contributions on the anatomy of tree growth. He does hope to give some idea of the range of current studies and, perhaps, of the need for prolonged programs of basic research on the course of growth throughout the year, the variations in that growth and its causes. Many workers have contributed to a growing body of knowledge, the following work being selected as typical: Anderson (1951) on tracheid length in conifers; Bannan (1941–42) on wood structure of *Thuja*, tracheid size and distribution of parenchyma cells; Barghoorn (1941) on the absence of rays because of specialization or unfavorable environments; Barrett and Downs (1943) concerning the effect of pruning on diameter and height growth; Bethel (1941) on the relation of maximum fiber length to height of tree among six dissected loblolly pines; Bruce (1951) on the

relation of height growth to fire and soil quality; Cook (1941a, b) on the period of height growth in ten conifers and six hardwoods in New York in which he found that the shape of the growth curves is constant, appears to be characteristic for each species and is not affected materially by temperature or rainfall unless it be drought; Downs (1943) on release of white pine in the southern Appalachians from a hardwood overstory; Gindel (1944) on false rings in Aleppo pine of Palestine as a result of interspersed periods of favorable and unfavorable growing conditions outside of the regular dormant season; Jacobs (1939) on the reduction of diameter growth near the base of a tree by prevention of sway; Ladefoged (1946) on the increase of diameter growth with an increase in crown size in the spruce of Norway; Lommetzsch (1940) on tracheid length and differences of lignin content between Germany and western Norway; Meagher (1943) on height growth of piñon and juniper seedlings little influenced by shade or watering; and Wilde and Voigt (1948) on wood density in jack pine in relation to soil fertility and drought resistance, frost injury and parasite attacks.

PHYSIOLOGICAL STUDIES

BASIC NATURE.   Some time ago Illick (1915) stated that "Growth rings have a physiological origin ".   That is true today. Any work which neglects the physiological aspects is, we think, merely a preliminary approximation.   However, here we should feel presumptuous to infer an ability to review critically all pertinent literature.   Work has come to our attention and, where possible, we have applied it to our problems.   For the application of the great body of physiological knowledge to growth layers we depend upon the plant physiologist and the biochemist.

Kramer (1943) stated that: " Variations in the environment can produce variations in tree behavior or growth only in so far as they affect internal physiological processes and conditions of the tree ".   The behavior of trees depends upon the interaction of hereditary and environmental factors.   In 1948 Kramer wrote on plant physiology in forest research.   The hereditary potentialities of trees operating in an environment by means of internal physiological processes and conditions produce tree growth.   Much work remains to be done. Of this Thornthwaite (1940) was well aware. He wrote: " The problem of atmospheric moisture in relation to

ecologic problems is still far from being solved. When ecologists acquire a basic understanding of the process of moisture transfer between the land surface with its vegetation and the atmosphere, the inadequacy of present measurements of atmospheric moisture and the futility of attempting to determine relationships between simple functions of atmospheric moisture and physiological functions of plants will become apparent ".

One is loathe to give examples which illustrate a possible lack of basic knowledge of plant physiology and anatomy. Only two will be given, without comment. " The question of records of swamp trees is puzzling until one remembers that for growth the roots of a tree must take in food as well as water. Food is obtained ordinarily through breakdown of the mineral material surrounding those roots. For this, oxygen as well as water is necessary. If the interstices between particles of soil are so filled with water that almost no oxygen is present, the tree is stinted in food and hence will not produce as large a ring as though the soil were dryer " (Hawley, 1941). Or again we may read: " Just under the bark is the growing layer which produces one true ring per year. This ring consists of fairly soft wood made up of large cells which grow quickly in the spring and of smaller cells with dark, thicker walls which grow in the summer and whose extra thickness protects the tree in cold winter weather while it is not growing " (Senter, 1938).

The work of Veihmeyer (1927) symbolized the serious work involved in understanding physiological factors. In studying these factors students have ranged widely, from scepticism on the influence of the moon (Beeson, 1946) to emphasis on the importance of growth-promoting substances. Apparatus has been devised (Studhalter and Glock, 1941, 1942) and programs organized (Glock and Studhalter, 1941) for the purpose of tracing the course of growth throughout the year. Food reserves and nutrient ratios have been emphasized by Asana (1950), Blackman and Wilson (1951), Friesner (1943b), Gibbs (1940), Handley (1939), Hull (1952), Humphries (1950), Judkins (1949), McComb and Kapel (1940), Mitchell and Chandler (1939) and Turner (1943), although none has excluded the influence of other factors. For instance, Handley found that chilling to near freezing brought radial growth almost to a standstill, impeded the movement of

starch from leaves, and cut down water conduction to the wilting point.   Available water either as soil moisture or rainfall, or other external factors, has been studied by Friesner (1943b), Friesner and Friesner (1941), Kramer (1941, 1944, 1945, 1950), Scofield (1945) and Thornthwaite (1945b).   With respect to rainfall, Friesner said that " it is apparent that tree growth reflects rainfall only when the latter is such as to influence the physiological processes of the tree ".   Kramer gathered together much information on soil moisture.   As soil moisture declines, the effects of such decline are exaggerated; he stated (1941) that: " The results . . . indicate that water probably is not equally available to plants over the range from moisture equivalent to wilting percentage, but becomes less available with decreasing soil moisture ". This may have importance because " almost everywhere soil moisture is sometimes deficient " (Thornthwaite, 1945b).   Internal factors were stressed particularly by Friesner and Walden (1946) and by Kienholz (1934–35).   Stone, Went and Young (1950), becoming interested in Coulter pine of southern California, which can survive long periods of drought on shallow soils, found that aerial parts took up water from the atmosphere— negative transpiration.

GROWTH-PROMOTING SUBSTANCES.   Growth-promoting and inhibiting substances are occasionally referred to by some investigators as though they give us a final answer to our questions about growth.   This is not quite true.   We still want to know how the substances act and what factors control them.   From the complexities involved in the production and application of growth-promoting substances to the apparent simplicity of comparing tree growth and rainfall there is seemingly a large gap.   However, we would be grossly unfair if we assumed that a student is unaware of the action of auxins and enzymes simply because he does not treat them at length in each of his writings.   Much detailed work has appeared on growth-promoting substances, and the pages of this magazine have carried valuable reviews.   Mention will be made here chiefly of those works which refer to growth-promoting substances as an adjunct to their prime interest.   Among these are Aaron (1948) who spoke of the effect of enzymes on cambial activity and solution of stored foods; Ashby (1950) who studied the action of hormones or the level of some nutrient on the meri-

stems; Avery, Burkholder and Creighton (1937) who considered a hormone as a cambial stimulus; Baird and Lane (1947) who found a double peak in summer in seven out of ten species of wild plants; Brain (1940) who found that external factors could influence auxin direction into a transverse stream and thereby influence secondary growth; Chowdhury and Tandan (1950) who distinguished between two types of auxins, one to give extension and the other to give radial growth; Evenari (1949) who wrote on germination inhibitors; Fraser (1949) who studied the effects of heteroauxin on the development of the components of an annual ring; Friesner (1942b) who said that growth rhythms " are most likely due to internal physiological conditions, such as available hormones ", and (1943b) who thought that enzymes and growth hormones were responsible for modifications of the symmetrical grand-period curve of growth; Hackett and Thimann (1952) who studied increase and decrease of water uptake as influenced by auxins; Messeri (1948) who studied the relation between cambium divisions and growth-promoting substances; Reed and MacDougal (1937–38) who thought auxin induced cambium growth; and Wareing (1950) who studied the dependence of extension and radial growth upon auxins. Using a branch of *Pinus strobus,* Fraser (1949) prevented formation of densewood by application of β-indole acetic acid (heteroauxin).

Studies concerning growth-promoting substances may be of first importance to those who work with tree growth. Scientists, it seems, will be hesitant to accept the opinion of Abbott (1946) who said : " It is of little consequence that no one knows just how a tree is able to grow ". He was speaking of tree-ring work.

FRUITING AND SEED YEARS. Perhaps in our work on tree growth we have neglected the effects of fruiting and seed years. Even Antevs in 1925 wrote: " Abundant production of seeds causes a reduction of the radial growth during the seed year. The decrease in growth may extend to the following year and then be greater than during the seed year itself ". Two years later Büsgen-Münch called attention to the effects of the formation and ripening of fruit on radial growth of pine. Tovstoles (1938), said Hustich (1945), pointed out that minima in the curve of radial growth of pine in Ukraina depend on the seed year. Others who have been conscious of the effects of seed year or fruiting on

growth are Hall (1949), Hodson and Zehngraff (1946), Hustich (1941, 1948a, 1949), Pearsall on papers by Singh (1950), and Scarth et al. (1947). If a " seed year " is responsible for a thin growth layer, how can we distinguish it from one which is thin from alleged drought? Hustich (1949) referred to Renvall who said that the intervals between seed years near or at timber line were long and irregular, occurring more frequently in recent decades, at least three in 20 years.

CROWN SIZE. In general, crown size or total leaf area affects, through food manufacture, the amount of xylem laid down (Badoux, 1946; Burns and Irwin, 1942; Gevorkiantz 1947; Mowat, 1947). The same does not apply so well in the Southwest (Pearson, 1943, 1950; Wadsworth, 1942). Wadsworth stated that " the rate of growth of ponderosa pine is much more closely related to environment than to crown size or age ". Pearson (1950) stated the matter even more definitely: ". . . a relatively small leaf surface is sufficient to handle all the photosynthetic activity that the limited water supply can support . . .". Such information can assist to an understanding of the effects on xylem formation of natural pruning through storms.

GROWTH RATE. The subject of growth rates involves so many complexities that the writer hesitates to refer to it. A single point only will be mentioned, the distance over which uniformity prevails. Miss Hawley (1941) obtained log ends from sawmills in the Mid-West. As to location of the original trees, the mill men knew " at least the approximate area being cut over at the time, a section usually within a fifty mile radius of the mill ". One is then a bit startled to read: " The tree-ring areas have been found to be so large that this approximation of location is close enough for all the work except that of special botanical and ecological interest . . .". Lyon (1943) worked with evergreens in New England: " The agreement between sites is highest when the trees are of the same species and the sites are not many miles apart. A distance of 50 miles apart is not too great for this type of cross-identification under conditions involving no other factors such as coastal effects or differences in elevations ". In contrast with the above, MacDougal (1923) noted that " two trees within 20 meters of each other at the Coastal Laboratory, at Carmel, California, are so differently placed that one made a basal layer of

wood 8 mm. in thickness during the last season, and the other one a layer 0.75 mm. in thickness ". Thus the influence of local topography and drainage. Glock (1950), working with conifers in New Mexico, found moderate disagreement between species and between members of the same species: " Partial disagreement among the various trees, growth layer to growth layer, emphasizes a definite localization of site factors to each tree. Disagreement among the trees increased with increasing distance, distance measured in yards rather than in miles ".

INITIATION AND CESSATION OF GROWTH. Variation in the time of growth initiation and cessation is bound up so intimately with the factors, external and internal, causing or inhibiting such growth, that some attention must be given to the subject. In 1944 Burns warned of the " futility of using averages to describe physiological conditions in a plant habitat ". For instance, if one compares tree growth with a growth factor which includes the same time interval year after year while the growth period varies, one could hope merely for results approximating those derived from a knowledge of the precise time of impact each year.

The spread of opening and closing dates for growth has been reported by different workers, among whom are Bonck and Penfound (1944), Chowdhury and Tandan (1950), Cook (1941b), Daubenmire (1945–46), Daubenmire and Deters (1947–48), Fowells (1941), Friesner (1941, 1942c) and Giddings (1941). In India, Chowdhury (1940) observed that growth in trees of the same species began over a range of one to three weeks. Cook (1941a) worked with trees in eastern New York during 1940. For 16 species growth initiation was spread from May 7 to June 9; cessation ranged from June 20 to September 16. The period of growth varied from 35 to 101 days. Daubenmire (1950–51), using different races of ponderosa pine at a station, found a spread of at least five weeks in growth initiation and almost four months in cessation. Friesner (1942b) noted a growing season of nine weeks for *Fagus* in 1940 and only five weeks in 1941. Friesner and Walden (1946) studied two specimens of *Pinus strobus* for five years, 1941–45. In sequence for the years given, one tree began radial enlargement April 26, May 2, May 22, April 15 and May 26; the other tree began May 3, May 2, May 15, April 29 and May 5. Growth ceased on the first tree the week ending

Nov. 1, Oct. 31, Oct. 16, Oct. 7 and Oct. 6; on the second tree
for the same years Nov. 1, Sept. 19, Sept. 18, Oct. 7 and Oct. 6.
Kienholz (1941) divided his trees into short season and long
season, the former completing 90 per cent of their growth in 30
days, the latter 90 per cent in 60 days. MacDougal (1936) noted
among six species of trees a period of radial growth varying from
50 or 60 days to 133 days. Reimer (1949) measured radial en-
largement on five species and found the interval during which it
occurred to vary from eight to 19 weeks. Schulman (1945*b*)
collected increment cores in the Colorado River basin, and with
them as a basis he noted that the start of cell growth varied from
mid-May to early June.

Perhaps the variations mentioned above help clarify some of the
difficulties encountered in a rigid time comparison between growth
and the factors favoring it.

GROWTH RHYTHMS. The length of the growing season varies
all the way from 12 months in the tropics (Shirley, 1945) to two
months or so above 56° north latitude (Marr, 1948). " Annual
rings are found only in regions with climatic periodicity, an alter-
nation between cold and warm, or rainy and dry periods . . ."
(Hustich, 1948*a*). The alternation may cover a year or a portion
of a year. Fluctuations in growth factors are not necessarily on
an annual basis; moreover, temperature and rainfall are not the
sole factors having to do with tree growth. In so far as rainfall
is concerned it can be evenly spread over the year, it can come in
winter or in summer, it can be divided into two rainy seasons per
year, it can fall in quantities sufficient to maintain soil moisture
at a high level, or it can fall so infrequently that soil moisture may
drop below the wilting coefficient between showers. This is but
one factor. Perhaps growth does not wholly cease throughout the
entire body of a tree during any part of a year (Bell, 1940).
Fluctuations in any one of the host of growth factors or changes in
their interrelationships may well cause variations in cambial
activity and in rate of growth, amount of growth and times of
growth. If growth factors are actually growth factors, then growth
will result whenever they operate effectively; and that may be
once a year, or several times, depending upon the time of impact
and the speed of physiological and anatomical responses. Vari-
ations in process or structure have been noted, for instance, by

Baird and Lane (1947), by Friesner (1941, 1942*a*, *b*), by Hawley (1939, 1941), by Hummel (1946), by Kienholz (1934–35, 1941) and by Schulman (1945*b*, 1951–52*a*).

This matter of cambial rhythm has great importance in studies on the course of growth. A body of evidence has accumulated to show that the rhythm varies in amplitude from a degree so mild that the results are barely perceptible to a degree so intense that the results are sharply bounded increments of growth. In addition, the evidence indicates a rhythm whose wave length may vary from a year or more down to a matter of several days or less.

Southern pine has been reported (Byram and Doolittle, 1950) " to put forth two or more leaders during a growing season, which may last from five to eight months, depending on the latitude ". Except for minor disturbances radial growth did not show periodic spurts. Darrow (1943) made interesting observations on the ocotillo (*Fouquieria splendens*) which grew under two rainy seasons per year. At first terminal growth is fast and occurs yearly; on the approach of maturity it becomes more and more sporadic and ceases when the branches are ten to 15 feet in length: " During the years characterized by widely-separated storm periods within a rainy season, ocotillo plants may have several periods of foliation and defoliation ". Ordinarily the ocotillo leafs out twice a year, at the start of the winter-spring season and at the start of the summer season.

Daubenmire (1945–46), in studying trees at different altitudes in Idaho, found that ponderosa pine ceased growth in early July at his lower station because of abnormal heat and dryness. After a week of moderate temperature and showers the normal rate of growth was resumed. *Thuja plicata* at the lower station had two distinct growing seasons interrupted by a period of quiescence in late August. The second growing season began with the first showers of the rainy season. Daubenmire and Deters (1947–48) measured trees on the campus of the University of Idaho. Both deciduous dicots and evergreen conifers grew for a few days early in April, 1944, in response to a brief period of above-average temperature. Then the trees were inactive during two weeks of cool weather. A smoothed growth curve of *Pinus* would show no absolutely quiescent period all year around.

Fielding and Millett (1941) worked on diameter growth of

Monterey pine in Australia. At Canberra, with its dry tableland climate and irregular rains, the only clearly defined period of diameter growth was in the spring; in summer and autumn bursts of growth followed soaking rains. At Mount Burr with its more favorable forest climate and seasonal rains, there were two main periods of diameter growth, one in the spring and the other in the autumn. Important bursts of growth were associated with any soaking rains during the drought of summer.

Handley (1939) chilled tree trunks down to a temperature a few degrees above freezing for the season of growth and found that he had prevented thickening and lignification of the outer rows of cells. Tharp (1939) studied purple sage in trans-Pecos, Texas. The shrub " bursts into a profusion of rose-colored bloom any, and every time, from spring to fall, that sufficient rain comes to it ".

In southern California Reed and MacDougal (1937–38) noted a characteristic periodicity in the growth of shoots on citrus. A graph of cambial increments showed three peaks of growth. In West Texas, Glock (1951) observed the course of growth and found periods of cambial activity within a season which gave multiple growth layers. Reed (1928) studied lemon trees in southern California and, measuring growth from May 1 to October 23, found that 94 shoots had three distinct cycles of growth, whereas 17 had only one cycle. The one-cycle shoots paralleled the other shoots for the first four weeks of the season and then were completely arrested: " Annual fluctuations in the growth rate of plants are well known, but intra-seasonal cycles are less prominent ". As a final note on growth rhythms the work of MacDougal (1923) may be cited. In July, 1919, formation of wood in Monterey pine ceased at Carmel, California, when water in the soil dropped to five per cent. One tree was irrigated for two days. It resumed growth and put down xylem of greater thickness than that earlier in the season.

CAMBIAL INACTIVITY AND DEATH. Growth rhythms composed of alternating periods of high and low activity, or of activity and no activity, lead directly into the problems of cambial dormancy with respect to cell division and what tree-ring students call " missing rings ". By " missing " they no doubt mean absent on the cores or sections or parts of trees examined. There may be

room for serious question, certainly room for basic experimental work, whether the cambium can remain inactive as regards cell division throughout an entire season; that is to say, the cambium ceases division at the end of one growing season over the entire stem and does not resume until the start of the second season later. In many cases observed by the writer, the cambium did lay down new xylem cells whose detection required the high-power microscope and complete and at times serial sections. Can the physiological processes remain in the, so-to-speak, neutral condition of respiration only, with no new cells on the one hand and avoidance of death on the other?

Douglass (1946a) has referred to missing rings many times. One of the problems mentioned by Hawley (1939) was " the location of missing rings on specimens growing in locations so difficult for life that no growth was possible during dry years . . .". One is tempted to ask, Should we use trees growing under such conditions? Or again, Do normal trees in normal distribution grow in such situations? Schulman (1945b) has been much more conservative and hence may be physiologically closer to the truth. Yet he has said: " It has been well established that, with suffici-ently severe growing conditions, the cambium in various parts of the stem may ' go hungry ' throughout an entire growing season and no new cells of wood may be laid down ". Can the cambium go hungry without deleterious effects? Later he said (1951) that in " severe years much of cambial area may be entirely inactive in terms of new cell growth ". This to botanists may need further work. Surely such a statement should be based upon an inspec-tion of a high percentage of total cambium area. In Texas, Schulman (1951–52a) found locally absent rings to be very com-mon, based upon core samples. A number of cores had no out-side rings, although they were taken in November. How was this ascertained?

A cambium inactive over a long interval (if that is possible) brings up the question as to the causes, the mechanism and the possibility of death. Severe growing conditions have been cited above. Perhaps death of roothairs (Caldwell, 1913) is of impor-tance. According to Kramer (1950), wilting caused injury or destruction of roothairs and the stopping of root elongation. Re-covery was slow. Work of this kind with trees may be called for.

Fowells and Kirk (1945) clipped off the root tips of seedlings and found their survival rate lowered. Mowat (1947) pruned ponderosa pines to an extreme degree and reported apparent vigor little affected. When trees were chilled down to a few degrees above freezing for a whole season they still produced xylem rings (Handley, 1939), the chief effect being that the growth layer to a depth of four or five cells from the cambium was unlignified and the cell walls unthickened. Defoliation (Church, 1949) may cause suppression of rings, and at times three years of growth may be lacking on parts of the trunk in balsam. In spruce that recovered there was no indication of missing rings. Recovery took 12 to 15 years. However, trees may die six to ten years later because the rings are so narrow they can not " transport the required amounts of water to the crown ". Here again death may have been partly due to the death of absorbing rootlets. MacAloney (1944) worked on the management of jack pine in relation to root conditions, weather and insects. Vigor and condition of the trees used were important factors in amount of growth and in mortality. Defoliation by budworm was not of primary importance until the trees were otherwise greatly weakened. Rainfall records, from eight miles distant, showed ten years of about normal or better precipitation followed by 20 years of drought or near drought. Interestingly enough, " The growth in basal area in the best trees was progressively greater in each of the three decades considered, while that of the poorest ones decreased materially ". Feeding roots suffered great mortality during times of drought and high temperature, especially in 1936: " The death of the trees was very probably due, in the final analysis, to the drought in 1938 and 1939 ". Thus decadence and death of some trees were due to several causes climaxed by two years of drought. The other trees were vigorous and even gained in basal area progressively during two decades of drought. This work of MacAloney and of others in regard to drought effects through time is highly indicative. High mortality and forest retreat can be the consequences of short-time drought, especially where combined with other complications.

A step farther may be justified. Briegleb (1945) worked with ponderosa pine in Oregon and Washington, studying their responses as related to good and poor sites, and to low and high vigor: " Poor growth periods do not affect all tree classes to the

same degree ". Briegleb referred to the poor growth years of 1929–1938 as described by Keen: " Trees of low vigor classes suffered a greater relative reduction in growth during the unfavorable period than did the more vigorous trees ". Would this make for the so-called " sensitive " trees of some workers? But to continue: " Among the A- and B-crown trees the greatest reduction occurred in the older age classes, but among those having C and D crowns the greatest reduction occurred in the younger ages . . . . The effect of growth cycles is also more pronounced on poor sites than on the good ". Briegleb found that growth of various stands varied widely, variations mostly accounted for by differences in site quality, stand structure and volume per acre. But small differences remained: " Whether the . . . differences are due to more or less permanent factors, such as climate, soil, or topography . . . is unknown ".

Finally the work of Hansen (1938) must be mentioned. He worked with *Picea engelmanni* in Wyoming, where growing conditions were rather harsh because of thin soil, low soil temperature, high winds, and because of the fact that much precipitation falls as snow which melts and runs off while the soil is still frozen: " In these trees there is considerable ring width variation, and individuals also show considerable variation with one another for the same year ". Growth layers, Hansen said, were commonly very thin: 0.05, 0.09, or 0.13 mm. for as many as 15 years. These rings probably " represent the minimum amount of growth which can take place and yet maintain life in the tree ".

It seems clear that the problem of a cambium remaining inactive entirely or locally over a prolonged interval of years, or for one or two years, will bear further study. In summary, the point scarcely needs to be stressed that the physiology of tree growth includes highly complex processes and relationships, and can be neglected only at our peril.

TREE CLASSIFICATION. Foresters have classified trees for some time now on the basis of age and vigor in order the better to understand site quality, tree condition, volume yield and relationships in general between the tree and its habitat (Briegleb, 1945; Dunning, 1942; Gevorkiantz, 1947; Gevorkiantz and Olsen, 1950; Hornibrook, 1939; Keen, 1936, 1943; Pearson, 1946, 1950; Thomson, 1940; Wieslander and Jensen, 1946). It may not be out of the way to remark that an understanding of the forester's

point of view regarding age and vigor can be of great assistance to those working with tree growth in any of its phases.

GROWTH RECORD IN TREES

Perhaps this section should be entitled " How the growth record is used ". The remarks made about crossdating some years ago (Glock, 1941) apply with equal cogency now, and the writer would hesitate to add to the examples there given if it were not for the encouragement in the work of Dobbs (1951) and of Ruden (1945). Dobbs pointed out with great justification the over-simplification in much of the tree-ring work. For instance, we can well understand why he was disturbed when we read: " If you count the rings from the exterior of a tree back to its center, you discover not only the age of the tree but also the succession of wet and dry years through which the tree has lived " (Senter, 1938). Botanists and foresters, as Dobbs remarked, " have shown the least interest in the remarkable record which the tree leaves behind it in its wood. This is understandable, because it is they who are most likely to realize the complexity of that record ". One necessarily agrees with Dobbs. Tree-ring work has centered its attention on one ring character, its width, and on one climatic factor, rainfall. It may be that the statement of Dobbs, that " the width of the annual rings is one of the least reliable characters which could be chosen, either as an indicator of climatic change or as a means of identifying and dating individual growth layers ", could be enlarged to include growth layers from most habitats. A single feature, such as width of growth layer, may not adequately portray " the effects of a complex environment upon so complex an organism as a growing tree ". A table of ring widths or a graph of them " is a fantastically crude substitute " for the record embodied in the entire tree. As Zeuner (1951a) suggested, perhaps characters other than width may come to be used in tree-ring work in humid-temperate climates. This could well apply elsewhere.

In the matter of deriving past climates or predicting the future, the words of Landsberg (1947) come to mind: " An extrapolation leads to treacherous ground and even though it would take another half century to prove or repudiate a statement, the mental reservations are too numerous to make an attempt ".

Crossdating, or the matching of growth layers year by year

from one tree to another, has been held to be the vital key for deriving calendar dates and climatic records by workers in the Southwest. Trees or specimens whose growth layers do not cross-date are said to be erratic or non-climatic and hence are disregarded or rejected. If the approach were more from the botanical side, this insistence on crossdating would be more convincing.

CROSSDATING AS A CALENDAR BASIS

If crossdating were able to establish the annual character of a growth layer and if it were able to assure the true calendar date for each growth layer, we should have an ideal situation. Douglass as early as 1923 claimed that careful application of cross identification made dating of rings certain. In 1931 the same view prevailed. The same reliance on crossdating appears in the work of Antevs (1948), of Douglass (1946a), of Schulman (1945a, b, 1947, 1951, 1951–52a, b) and of Weakley (1943).

Antevs (1948) spoke of " absolute dates " obtained from tree-ring records and thus apparently accepted crossdating as the vital key. Schulman (1945b) used certain criteria to suggest the identification of false rings and then reached a solution by crossdating. In a discussion of the Colorado River drainage basin and its adjacent regions he stated: " It is obvious that there is throughout this transect of some 2,000 miles a tendency for persistence in chronology . . .". Such a statement is somewhat surprising from the ecologic standpoint.

In 1941 Douglass attempted to answer the criticism of Sampson (1940) : " Our criteria of climatic character in the ring records in our trees is not sensitivity (the amount of fluctuation in thickness from ring to ring) . . . , but crossdating quality which is of an altogether different nature . . . . Sensitivity is a secondary feature which is important only in the presence of crossdating ". In spite of this he went on to say: " If there is no sensitivity there can be no patterns and therefore no crossdating by patterns . . .". It seems in other words that sensitivity is secondary to the feature for which it is directly responsible—a difficult piece of logic.

Will (1946) depended more upon judgment than upon measurement and dated rings within four or five years. Weakley (1943) depicted his chronologies on skeleton plots. Out of 400 years, 46 per cent showed below-normal growth.

Crossdating, as heretofore mentioned, has been held to prove the annual character of a growth layer. All trees or all specimens in a collection, however, do not necessarily crossdate. If growth-promoting factors operate to produce more than one sharply bordered growth layer per year on occasion, is it not possible that they do so in many trees of a stand (Glock, 1951)? Is it not more important to trace the course of growth by experiment and prolonged observation than to attempt to apply simple but arbitrary criteria, as sharp border and width of growth layer?

QUALITY OF CROSSDATING

The fact of crossdating is one thing, the quality is another. But before quality is considered a word must be said about the " eye and judgment " method devised by Douglass whereby rings are dated and crossdated by means of a handlens. Douglass has tried earnestly to teach his method to others, not always successfully. He learned to recognize by sight characteristic narrow rings, patterns of narrow and normal rings, and sequences. The method once grasped is rapid, reliable and, what is more, enjoyable. Not so to Gladwin (1940b) who called the method subjective: " There are some of us, however, who have run into difficulties and . . . the first question which arose to plague me was how to decide the elementary question of when is a ring narrow ". The writer (Glock) has had the same experience as Douglass in teaching his method to students; most grasp the method rather quickly, but occasionally an individual does have difficulty. Gladwin devised a new method which employs all rings, but after consideration the writer prefers the Douglass method. So far as can be seen, the fundamental weaknesses, if such exist, are identical in the two methods. The Douglass method has seemed and does seem highly reliable for crossdating; its weakness lies in whether or not it establishes the annual character of a growth layer.

Bannister (1951) worked with Douglas-fir and ponderosa pine in the Gallina area, New Mexico. The graphs of the widths of five specimens show 21 parallel trends and 49 opposite—not very good correspondence. So far as the means of the two species are concerned he stated that their chronologies are essentially the same, and yet the graphs showed 58 parallel and 22 opposite trends. He compared his trees with those of Mesa Verde, 120

miles northwest. The Douglas-firs had 64 parallel and 26 opposite trends. The Douglas-firs of Mesa Verde versus the ponderosa pines of Gallina had 52 parallel and 28 opposite trends.

In Mesa Verde National Park Douglass (1942) took Douglas-firs from the side of a canyon, a site favorable to crossdating, he said. A span of 100 years taken from his chronology gave 73 parallel and 27 opposite trends.

Later (1946b) Douglass also reported on single trees from Mesa Verde. Two trees showed 50 parallel and 25 opposite trends; a different two had 56 parallel and 19 opposite trends. Seven trees showed 40 parallel and 35 opposite trends. Of these trees Douglass said: " This crossdating indicates climatic effects and gives a near record of precipitation in that region ". Some will have difficulty in accepting the plain statement. Moreover, it is interesting, in view of the inconsistencies among the trees at Mesa Verde itself, to compare these results with those obtained by Bannister where he compared trees 120 miles distant with those from Mesa Verde.

Eidem (1943b) compared a curve of 14 trees from Trondheim, Norway, with a mean curve from Selbu, a valley some 50 km. distant, and obtained a correlation of 0.74 ± 0.05.

Friesner (1950) found mixed results in Indiana. Two members of the same species might have high agreement (i.e., 89 per cent), whereas another two might have low agreement. In the general picture he recorded agreements ranging from 22 to 89 per cent. Averages ranged from 46 to 62 per cent agreement.

Giddings (1941) gave graphs of tree groups from two to 500 miles apart in Alaska. In the " actual dating " of driftwood its graph showed 39 parallel and 26 opposite trends with one recent sequence, and 48 parallel and 17 opposite with another sequence. A comparison of the driftwood with both sequences gave 35 parallel and 30 opposite trends. The two wood sequences themselves gave 46 parallel and 19 opposite trends. So much for dating the driftwood. In so far as recent trees are concerned Giddings said that the same ring records existed as much as 150 to 200 miles apart. Two groups of five trees each, two miles apart, gave 41 parallel and six opposite trends, which is very good. Two groups of five trees each, 30 miles apart, gave 104 parallel and 34 opposite trends. A third group of ten trees, 50

miles away, added to the previous gave 29 parallel and 18 opposite trends. Two groups of 25 and 11 trees, 200 miles apart, gave 60 parallel and 40 opposite trends. When two groups of 28 and 10 trees 200 miles apart were compared with the previous groups 500 miles away, the results gave 29 parallel and 71 opposite trends. At best all of these results clearly indicate increasing divergence among trees with increasing distances.

Glock (1950) worked with tree cores from four species from the upper part of the ponderosa pine zone in northern New Mexico. Crossdating was practically nonexistent, and therefore measured ring thicknesses were compared. Expressed in percentage, individual trees in rather compact groups varied from 60 to 89 per cent in their agreements with each other. When the measurements were divided into two intervals, 1850–1897 and 1898–1941, the earlier interval always had the higher percentage of disagreement.

Hansen (1940) took cores from fir and spruce on the Medicine Bow Range of southern Wyoming and found crossdating relatively easy. However, the two species were only in " fair correlation " with each other: " Also the general trends from higher to the lower and from the lower to the higher points are somewhat in agreement ". These are modest statements. In 1941 Hansen reported on his work with three species of conifers from central Washington. He tallied the years of agreement between each two species and found a variation from 37 to 41 out of 80 years.

Hustich (1945) used the novel method of correlating volume growth with radial growth and obtained a coefficient of 0.63 ± 0.14. In northern Fennoscandia Hustich (1948a) found coefficients of 0.74 to 0.83 for groups 140 to 190 miles apart, but when he compared this with trees from the coast of Norway the coefficients dropped considerably. He found (1948b) the curves of growth in Lapland and Oregon almost the reverse of each other, and apparently frowns upon such long distance correlations (1949).

Lutz (1944), who studied two species of swamp conifers in Connecticut, noted a close agreement of maxima and minima between his trees and those of Lyon from mesophytic sites.

Lyon (1943) studied conifers within a short distance of Boston, conifers chosen as typical of their sites. Graphs of two groups

gave trends with 74 parallel, 36 opposite, and 17 with one entry giving no change.   For purposes of dating unknown sequences Lyon used a master calendar made up of maxima and minima in which practically every ring was noted.   Six groups of eastern hemlock (Lyon, 1946) widely distributed over New England gave " somewhat uncertain " crossdating.   A sequence of at least 100 rings to be matched against its own local chronology was judged necessary for dating.

Among conifers on the east coast of Hudson Bay near the forest-tundra border Marr (1948) found satisfactory crossdating between groups 80 miles apart.   The incidence of first class narrow rings came out two in 159 years ; second class gave eight. This resembles very much the character of the growth layers obtained by Glock (1950) centering at 9000 feet in New Mexico.

In Arkansas Schulman (1942a) chose trees from ridge tops. Junipers and pines taken from sites said to have poor drainage possessed sequences which were erratic and devoid of sensitivity ; they were not used.   Previous collections from the Mississippi Valley region, he said, had shown poor crossdating, and hence better field selection was needed.   It is of interest to note that Schulman found most of the ring variation in the densewood, little in the lightwood : " The latewood curves . . . show that much of the crossdating in the total ring is traceable to the latewood ". Because of this he devised a " secondary index of growth ", the " inter-season or L/E ratio ".   By inter-season does he mean between seasons or within a season (intra-season) ?   What do we have ecologically, that the densewood does not give us, when we obtain the ratio of densewood with character to lightwood without character ?   A test of the L/E ratio on six trees, 1860–1940, appeared to give very poor agreement.   On the whole the results achieved with trees selected as above described must be viewed in the light of the work of Turner (1936b, 1937).

Schulman (1945a) worked with Douglas-fir and ponderosa pine in the Pacific Northwest.   Nine Douglas-firs were compared with 17 ponderosa pines and the results spoken of thus : " In Figure 2 it is shown that Douglas-fir of the semiarid Northwest carries essentially the same chronology as ponderosa pine ".   An analysis of the graphs of his Figure 2 gave 88 parallel and 54 opposite trends.

In his work on the Colorado River basin Schulman (1945*b*) covered a large territory. Graphs of tree growth were given for different tributary drainage systems; from these a test decade, 1851–1860, was selected for analysis with results as follows: Green River trees had three parallel and seven opposite trends; Colorado above the Gunnison, six parallel and four opposite trends; Gunnison, two parallel and eight opposite; Dolores, five out of ten parallel; and San Juan, four out of ten parallel. Schulman also assembled tree-growth records into mean curves for Douglas-fir, ponderosa and limber pines, and piñon, from the lower forest border. When analyzed the curves gave the following trend relationships:

Douglas-fir vs. pines .... 48 parallel, 12 opposite
Douglas-fir vs. piñon .... 43 parallel, 17 opposite
Pines   vs. piñon .... 40 parallel, 20 opposite

Schulman (1947) collected extensively in southern California in order to extend gauge records of runoff backward in time. In bigcone spruce crossdating quality was at its best and the correlation coefficient between two of the trees came out 0.84. Among the five trees of the group, trend analyses ranged from 109 parallel to 94 out of 120 years. All five compared gave 84 out of 120 parallel. These figures are high when we consider the complex nature of tree growth, but whether they are sufficiently high safely to extend gauge records of runoff is a different matter. Collections also included groups of different species—white fir, western juniper, piñon, ponderosa pine and bigcone spruce. Interspecific trend comparisons ranged from 67 parallel to 47 out of 80. When all five are compared the trends were 33 parallel and 47 opposite. Other groups, inter-specific and intra-specific, ranged from 54 parallel to 38 out of 80. When the five are compared the trends were 15 parallel and 65 opposite. A word must be said about what Schulman called " obscure chronologies ", those showing poor crossdating because evidently they were " dependent primarily not on one element such as available water " but upon the entire complex of growth factors. Trend comparisons come out only slightly less favorable, if any at all, than those previously cited. Finally Schulman presented graphs as a transect for 1400 miles of the Pacific Coast in order to study possible systematic

shifts in dates of maxima or minima with latitude. " No reliable tendencies of this type were found ".

More comparisons of the same kind could be cited but one more must suffice. Schulman (1951) reported no significant relation between tree growth of British Columbia and that of Colorado River basin for the last three centuries, which is not unexpected. The correlation coefficient between tree growth of the Colorado River basin and southern California was 0.46, for 1650 to 1935, and between the tree growth of the Colorado basin and eastern Oregon it was 0.21.

In summary it will suffice to say that the examples of cross-dating bear out the fact that tree growth varies from tree to tree and depends upon the interaction of a host of factors, internal and external. The examples illustrate what has been said before in relation to selecting a single feature, such as width of growth layer, to epitomize the total response of a tree to its environment. In the comparison of two growth layers, no matter where they may have been grown, there are only three possibilities: they are of equal width (where measured) or one is thinner or thicker than the other. Does crossdating solve as many problems as some workers maintain?

STATISTICAL CORRELATION

Caution in the use of correlations has been urged by various students (Dobbs, 1951; Glock, 1941; Jones, 1943; Lyon, 1943; Pearson, 1941; Sampson and Glock, 1942). Little need be added.

Jones quoted Keynes as saying that " sensible investigators only employ the correlation coefficient to test or confirm con-clusions at which they have arrived on other grounds ". Glock (1942c) devised a method of correlating continuous time series by combining direction of variation from year to year with amount of that variation into a trend coefficient. Very probably a list of the number of parallel trends and of opposite trends gives a simpler and clearer picture of what tree growth and certain factors are doing from year to year. Lyon (1943) relied upon critical years only. Glock (1950), Hansen (1941) and Miller (1950) used essentially an enumeration of parallel and opposite trends.

In 1942 Schulman (1942a) refrained from using correlation coefficients and spoke of trends. In 1945 he (1945a) rejected the

use of the coefficients but gave values of r anyway because they are so well known.   Another article (1945b) of the same year gave values of r apparently without comment.   Later (1947, 1951, 1951–52b) he continued the use of correlation coefficients, which is not too objectionable if readable graphs are published.

The danger that correlation coefficients may be a hindrance instead of a confirmation of prior fundamental work is vividly emphasized in the following: " The result of this procedure is a correlation coefficient which indicates the effect of precipitation upon growth of that species in that area, and by use of it pre-cipitation of the past before weather records were kept may be figured from tree growth of the past, with measurable percentage of certainty " (Senter, 1938).   No better brake can be placed upon the possible misuse of statistics than the apt words of Dobbs (1951) : " Fortunately, in the realm of tree-ring studies, the phase of inexpert or ill-considered resort to statistics appears to be on the wane ".   Statistics do not tell us things we did not know: " At most, it might justify a guess that rainfall and tree growth are not entirely unrelated ".

CROSSDATING AS A BASIS FOR CLIMATIC INTERPRETATION

Crossdating has been held by some not only to establish the annual character of each sharply bordered growth layer which can be traced into more than one tree but also to establish a climatic record, especially either of rainfall or temperature.   The technique embodied in collection and crossdating promote " long tree-ring indices of maximum fidelity to a single element, such as seasonal precipitation or runoff " (Schulman, 1945a).   In fact " The ulti-mate objectives of the studies at the Tree-Ring Laboratory are (1) the mapping through tree rings of the mean seasonal atmos-pheric fluctuations year by year, for many centuries, over the entire world in all forested regions, and (2) the interpretation of such chronologies in terms of possible solar or other extraterres-trial forces and their use as aids in long-range weather forecast-ing ".   This surely was an ambitious program, and one wonders why botanists, foresters or meteorologists have not long since begun the same work.   The answer no doubt has been given by Dobbs (1951) as quoted heretofore.

Concerning crossdating as a more or less magic formula, Dobbs

has said: " There is no more reason to suppose that trees which cross-date give a better picture of climatic variations than those which do not; on the contrary, they are more likely to give a distorted one, simply because they are selected for coincident features, some of which may well be non-climatic in origin ". Such remarks are seemingly rather severe, but they come as a natural reaction to the insistence that crossdating is the key to all so-called tree-ring work (Douglass, 1941, 1945a, b; Hawley, 1941; Schulman, 1942a, 1943, 1945a, 1951, 1951–52a, b). Insistence on the climatic value of crossdating came out in the words of Douglass (1946b) : " We found that the best ring records came from sites of limited and discontinuous water supply and that the identity of climatic trees was established by definite crossdating. Thus crossdating between many trees is itself the evidence of the climatic origin of the dating features ".

Some workers have found that different species differed from each other in certain respects or that each had its own chronology (Burns and Irwin, 1942; Douglass, 1931; Giddings, 1941; Hawley, 1941; Huber, 1948; Lyon, 1943; Miller, 1950; Schove, 1950; Schulman, 1947). At places these differences are intraspecific. If two or more chronologies exist in the same area, which one gives a faithful record of climate? This was a problem which beset Miss Hawley (1941). A few of her statements were rather severely criticised (Glock, 1942a, b). When we are confronted by such a problem perhaps it would be better if we were to go back and begin with fundamentals, in this case the physiology of tree growth, rather than to proceed forward.

Attention almost exclusively to trees, which crossdate, from the lower forest border, and rejection of trees from near the forest interior (Douglass, 1941, 1946a) do not harmonize too well with the proposed program of mapping all forests of the world in order to obtain mean seasonal atmospheric fluctuations year by year (Schulman, 1945a). Apparently crossdating is at its best at the lower forest border where atmospheric factors fluctuate with a rather high amplitude. Even here the sites must be especially unfavorable. Douglass (1942) studied Douglas-firs on the side of a canyon in Mesa Verde National Park and noted the location as " an unusually dry site and one favorable to crossdating . . . in this dry area the precipices above and below, the

steep slopes of the grove area and the unfavorable tilt of the mesa above and the sedimentaries at the back of the grove, compel these trees to subsist on the precipitation that falls on their own area. The available water for the trees is close to a minimum ". Again we read (Douglass, 1946a) of a tree " on a high isolated point or growing in a crack in a rock or thoroughly protected from any ' imported ' water ". These examples must suffice to indicate not only the insistence upon the lower forest border but upon very unfavorable sites such as steep rocky slopes within this dry area.

At first one is somewhat confused by the distinction between sensitivity of rings due to violent fluctuations in a growth factor and non-sensitive rings which have an erratic record. Schulman (1942a) spoke of groups of pines and cedars as being erratic and lacking in sensitivity, and therefore they were not used. In 1943 Schulman wrote " of violent fluctuations of ring widths (high ring sensitivity) " in trees whose rings were dated by cross-dating. In 1945 (1945a) Schulman wrote more in the same vein : " in the dry Southwest the most useful chronologies are found in long-lived conifers of nonerratic growth characters situated on steep slopes underlain by pervious rocks, so that moisture conservation by the soil is at a minimum, and near the dry or lower forest border . . .". Farther along he wrote concerning sensitivity and asserted that " in cross-datable ring series the violence of the year-to-year fluctuations in ring widths is directly proportionate to the indicator value of the chronology ". The more violent the fluctuations, the greater is the value. After careful consideration the reader concludes that a sequence which has violent fluctuations is sensitive if it can be crossdated, but erratic if it cannot be so crossdated. This sounds extreme and one really doubts that Schulman meant to go so far. Contrary to the concern of Douglass (1946a), the people of the eastern seaboard may not be unaware of the dryness of the Arizona region, of the effects of two rainy seasons a year, and the principles governing the income, retention and outgo of soil moisture.

Exclusive adherence to the process of crossdating has very nearly restricted the workers in the Southwest to lower forest border trees, trees growing under conditions adverse even for such a zone. Yet others, notably Burns, Dobbs, Daubenmire, Friesner, Glock, Hansen, Hustich, Huber and Lyon, have achieved

a measure of success at least from the ecologic standpoint in their studies on trees from more normal sites and from more humid climates. Hawley (1941) has grasped the fact that in all probability trees in the more humid regions are sensitive to environmental changes under which they grow in much the same fashion as those growing in the drier regions. Friesner in Indiana and Lyon in New England have made worthwhile contributions to our fund of botanical knowledge. Glock (1950) studied tree growth at the upper part of the ponderosa zone well within the forest interior and found close correspondence to growing season rainfall. He chose normal trees from sites normal to the area: " . . . the locations were chosen so that abnormal drainage toward or away from the trees was at a minimum ". Steep rocky slopes with highly adverse conditions at the lower forest border were avoided.

CROSSDATING AND DATING APPLIED TO ARCHAEOLOGY

Hack (1942), in his studies of the physical environment in the Hopi country of Arizona, accepted tree-ring dating apparently without question. In addition he referred to droughts as revealed by tree rings; but other factors besides a lack of rain can restrict tree growth. Schulman (1948b) worked out a tree-ring index in the Uinta Basin of Utah back to 379 A.D. with the help of ancient beams. This index, he said, ran essentially parallel to the indices from Arizona. Will (1946) in North Dakota based a master sequence on one oak.

The whole matter of dating by tree rings is of much concern to archaeologists because they must be sure of the botanical foundation of tree-ring dating, of the method of extending master charts into the past, and of the method of crossdating an unknown by means of the master.

Hawley (1939) had experience with charcoal fragments averaging not over one inch in diameter and containing from two to 100 rings. Pieces with less than 30 rings were useless. If one fragment showed bark, the rest could be dated. If no fragment was complete, " then there is no recourse but to hazard an estimate of the final date, based on examination of ring curvature and of the growth increment ". This is dangerous ground; how can ring curvature indicate the number of rings *outside* the specimen and worn away? As to dating onto a master chart, Hawley (1941)

stated: "All that can be said about the actual date of any set of specimens which cannot be matched into a master-chart is that they must antedate the earliest period represented by that chart". Such a conclusion will be a surprise to ecologists. In the same report Miss Hawley revealed that pine and hemlock of the same area did not crossdate. It is difficult to reconcile the two statements. She did say that dating by one specimen is unsafe, and yet one master chart was based on one oak specimen from 1536 to 1659. Smiley (1951) had this to say: "In spite of the fact that many prehistoric sites are located near or on the forest border, the percentage of dated specimens is very low in ratio to the total number of specimens collected. Species of undatable quality were often used in construction as were trees of a datable species which grew under conditions that did not allow the recording of precipitation changes. It is estimated that between 5 and 10 percent of the total specimens collected have been dated". It seems that Knipe (1942) dated a specimen of pine charcoal from a site in southern Arizona as 1243 to 1274. The piece contained 32 rings and was dated on the basis of the rings for 1263 and 1269 which were preceded by four large rings forming a strong "signature". Colton (1945a, b, 1947) found it necessary to revise the date of the eruption of Sunset Crater in northern Arizona from 875–910 A.D. to 1046–1071. Tree rings and pottery types were used in conjunction.

In 1932 Gladwin (1940a) attacked the problem of tree-ring dating and became sceptical not only of what he called the subjective methods of Douglass but also of the validity of much of the dating. His results have been published in a number of articles (1940b, 1942, 1943). Antevs has given a review of another work (1946). Soon after 1936, Gladwin stated that Flagstaff dates were "brought into question" (1942) and he objected to the method of assigning outside dates to specimens lacking outside rings. Gladwin (1943) doubted the accuracy of dating specimens on a small portion of a master chart hundreds of years long. He was of the opinion "that the pattern of tree growth is often repeated over short periods of 25 years or so, and it is quite possible that such repetition may occasionally be of longer duration . . . . As I have said before . . . I have more faith in archaeological evidence than I have in tree-ring dating . . .". Because of the possible recurrence of ring sequences, Gladwin suggested the use of archaeological evidence to determine the general age of the

period and then the use of tree rings to give a more exact date within the period.

Until we know more about the course of tree growth within a season and from season to season, the factors internal and external that motivate growth, and the accuracy of the methods used in setting up a master chart, the Gladwin method appears to be a sensible and just expedient. But it also assumes a master chart of absolute accuracy.

RADIOCARBON DATING TESTS

Age determinations by radiocarbon analyses have been made to a greater and greater extent during recent years. To mention a few who have given attention to method and trial dating there are Deevey (1952), Flint (1951), Flint and Deevey (1951), Libby and Arnold (1950) and Zeuner (1950a, 1951b). Various cautions have been put out by Bartlett (1951), Childe (1950) and Flint (1951).

An interesting aspect of the dating comes out in connection with the analysis of certain tree-ring samples with which the present writer is acquainted. If the radiocarbon dating is very nearly correct and no contamination has occurred, the age of the sample is highly suggestive. A specimen of Douglas-fir wood obtained by Morris in 1931 from Red Rock Valley in northeastern Arizona was analyzed (Arnold and Libby, 1949, 1951) and gave an average age of 1042 ± 80 years, whereas the age based upon tree rings was 1370. Arnold and Libby (1951) commented: " Looks low versus expected 1370 ". Reference to the ages of other samples (1949) determined shows that the radiocarbon ages very nearly equalled or exceeded the expected ages. Only the tree-ring sample showed such a low age in comparison with the expected. Although the difference may not be statistically significant, one wonders about the accuracy of the tree-ring master chart which was built up on many specimens (in most cases) from trees that grew at the lower forest border. This is the environment where adverse conditions prevail, where high amplitude fluctuations characterize rainfall, soil moisture and other growth factors, where the greatest sensitivity exists, and where cross-dating is at its optimum. It is also the zone where it has been found (Glock, 1951) that multiplicity is a characteristic feature of

the annual increment. Glock has estimated the multiplicity at zero to 15 per cent with an average of five or six per cent, on the basis of trees growing away from the lowest forest border, and therefore those trees may have had less multiplicity than some of the materials procured by the Indians and later used in construction of the master chart. It is conceivable that further study will show that the quality of crossdating up to a certain optimum is directly proportional to the percentage of multiplicity.

GROWTH AND CLIMATE

No very startling results have appeared concerning tree growth and climatic factors since the first review (Glock, 1941). A few investigators have published rather extensively on climate as derived from tree rings, whereas the vast majority of botanists, foresters and ecologists has been primarily interested in tree growth as such and the factors, external and internal, which regulate it. It is rather generally agreed that soil moisture, because of its wide fluctuations, has great importance to trees near the borders of arid lands and that temperature during the growing season, because of its impact on physiological processes, has great importance to trees near the borders of cold regions. Nor should the probable role of growth-promoting substances be entirely neglected.

Particular emphasis has been given by some to the accuracy with which the widths of tree rings record rainfall. Whether or not such a position is justified will perhaps become apparent later. For instance, Douglass (1941) claimed that " If many independent trees in a forest over a wide area and for a long interval of time show similar ring variations in identical years, the cause of such variations is climate because climate is the common continuous factor in their surroundings ". If we are not mistaken the area referred to is over hundreds of miles and refers especially to rainfall. How this fails to harmonize with the variations of habitat factors, even in short distances, is difficult to understand in the light of much ecologic and meteorological work, as, for instance, that of Croft and Marston (1950), of Visher (1946, 1950) and of others previously cited. Dobbs (1951) has given us an extremely penetrating and lucid analysis of the difficulties inherent in the use of simple ring widths as true

records of single factors and has listed many factors which may intervene at any point from rain to cell formation to affect the growth processes: " Even in a dry climate the relation between rainfall and the activity of the cambium is far from simple and direct ". Any drought sufficiently severe will of course limit cambial activity: " But it is another matter to assume that every narrow ring represents a drought, or that every broad ring represents a wet year ". As a matter of fact, " At present the only undeniable record of climatic effect upon the wood is the frost ring . . .". Much of what Dobbs says is highly pertinent, but lack of space forbids further elaboration.

Douglass (1946b) extended his claims by stating that growth curves " supplement the observed meteorological data by providing . . . a length of record many times that of the longest meteorological series . . .". Extension, not only into the past but also into the future, was proposed by Hawley (1939) with the further suggestion that amounts of rainfall might also be computed. According to Meyer (1951), statistical analysis indicated that 90 to 95 per cent of yearly growth variations were due to weather. Trees near the dry lands (Schulman, 1945a) are " natural gauges " which continuously record " fluctuations in annual precipitation and runoff ", and those near Arctic regions are " living thermographs ". No one apparently has ventured further than this.

The complexity of the relationships has been mentioned by Brooks and Kelly (1951), Lyon (1943) and Marr (1948). Meissner (1943) in Germany and Pearson (1941) in northern Arizona found no or little relationship between rainfall and tree growth. Graves (1946) described the complications in the weather of an unusual spring in northeastern United States with its early warm period and subsequent cold wet interval which caused root rot and a blight on one species. In central Europe Huber (1948) reported that rings are narrow both during dry summers and after cold winters.

Hustich (1948a) has done much of his work at the northern forest limit in Europe. There " the trees react closely to the smallest changes in climate ". He has introduced what he called the climatic hazard coefficient (1947, 1948a, b, 1949) which is the degree of variability in growth caused by annual changes in climate. The coefficient in percentage is essentially the standard

deviation divided by mean temperature of the particular period. Hustich found that the coefficient decreases from north to south in Finland. Brier (1948) commented on the work of Hustich and emphasized a possible correlation between tree growth and mean annual hemispheric pressure.

In his careful synopsis of tree-ring work, Zeuner (1951a) has well summarized the problem: "Thus there is no doubt that temperature and precipitation do influence the growth of trees to a certain extent, though not exclusively and not everywhere in the same manner. A great many tree-ring records, in fact, show no distinct relations between precipitation or temperature, and the thickness of the rings ".

GROWTH AND TEMPERATURE

For some reason temperature correlations do not seem to be so attractive to workers as do those of rainfall. None the less, positive results in any region would have a usefulness equalling that of rainfall correlations. Cook (1941b) found little relation between tree growth and either temperature or rainfall in eastern New York.

For a number of years Friesner carried on fundamental research in tree growth in Indiana, and we are indebted to him for much sound information. In a summary of a portion of his studies Friesner (1943b) remarked: "Temperature plays its most significant role in determining the time of initiation of growth but shows only an obscure and indirect relation to the quantity of growth. Of course, it must be remembered that the response of the organism is to the sum total of its environmental conditions and that temperature is a part of this total ". In lower latitudes the relation is mostly inverse, whereas it is direct in the higher.

The following work has found a relation more or less between tree growth and temperature. It has been reported that Akerhielm (1940) noted that a small increase of temperature brought about a remarkable increase of radial growth of old pines in the north of Europe.

In Norway Eidem (1943a) held temperature of the growing season to be a leading factor in determining ring thickness in fir. Neither summer rainfall nor the preceding winter rainfall had an appreciable effect.

Giddings (1941) in Alaska was troubled by finding more than

one chronology. A spruce chronology on a gravel terrace differed from surrounding trees and gave a radical departure from the usual climatic reaction, being due perhaps to a combined rainfall and temperature effect. In contrast a different chronology—from timberline—gave good agreement with summer temperature. Trend analysis between June temperature and tree growth showed 21 parallel and eight opposite. Mean June temperature and a group of trees from Noatak had 17 parallel and 11 opposite trends; another group of 25 trees from Norton Bay had 17 parallel and 11 opposite trends. In comparison June precipitation and Norton Bay trees gave 14 parallel and 14 opposite trends. If temperature records could be made to match more closely the exact time of growth for the trees of the different chronologies (i.e., timberline and valley bottom), better correlation might be obtained. Later Giddings (1951) reported on two groups of spruce trees 50 miles apart and 80 miles from the weather station. The two groups showed 31 parallel and nine opposite trends. Compared with growing season temperature, June-July, each group gave 20 parallel and 13 opposite trends. Correlations of single trees were not very good. Perhaps when single trees are merged into an average, disagreements cancel out.

Hawley (1941) measured 23 pines, some of which came from central Georgia, others from southern Missouri, eastern Tennessee and Arkansas, and correlated them with yearly temperature at Cairo, Illinois. The coefficient, r, came out as 0.57. For oaks, r was –0.35. The negative correlation was surprising.

In reporting on the work of a student, Huber (1948) said that ring widths in the high mountains of Bayern correlated with mean summer temperatures, with mean noon temperature during the summer, and with duration of sunshine.

Hustich (1941, 1948a, 1949) has clearly shown the effect of temperature in northern Finland. From 1933 to 1939, radial and height growth, and needle length of *Pinus silvestris* followed the mean temperature of the warmest month (1941) : " At the northern pine-limit the temperature is the most important impeding factor " (1948a). Even a fairly small increase in temperature appeared to cause " remarkable rejuvenation " in the radial growth of old pines at the timber line. Hustich presented correlation coefficients to substantiate the temperature relations. Growth of pine cor-

related with temperature 130 miles away gave: for June temperature, 0.14 ± 0.17; for July temperature, 0.54 ± 0.12; for August temperature, 0.31 ± 0.16. For July the coefficient is "fairly good"; but other factors must be considered, such as the effect of temperature during the previous year on food reserves, leaf surface and seed production. Hustich understood the complexities of growth: " The radial growth of the pine is, however, not a simple consequence of the temperature of the summer months in which the annual ring in question is formed ". For tree records closer to the weather station, Hustich obtained radial growth versus July temperature, $r = 0.86 \pm 0.06$; cubic growth versus July temperature, $r = 0.61 \pm 0.14$. The difference between radial growth and cubic growth is of interest; correlated they gave 0.63 ± 0.14. As a summary Hustich said: " Generally speaking, in the northern part of the temperate zone the correlation between temperature and growth is stronger than the correlation between precipitation and growth ". One can scarcely object to such a conservative statement. How well the trees give us an accurate temperature record through the years is a different matter.

Ording (1941) has done much work in Norway. Analyses were made on 130 trees of *Pinus silvestris* from six moor and swamp localities and on 50 pines and 90 of *Picea abies* from five productive forests. Correlations with temperature records from 1821 to 1920 showed wide rings of spruce and pine in warm summers and narrow rings in cool summers. But exceptions were frequent. Temperature of the preceding summer may also have an influence. Standard scales, Ording recommended, should be built for each species and for individual climatic regions. Spruce and pine in the same stand did not crossdate.

Schove (1950) has worked with tree growth in Scotland and has obtained important results. Dating by means of tree rings had three limitations at the start: it should be confined to one species at a time, to one climatically uniform area at a time, and should be corrected for age by a single objective method. In Scandinavia and in Scotland, rainfall and snowfall regimes vary considerably from place to place, and there was difficulty in cross-dating pines near one fiord with those of a neighboring valley. More than one tree-ring series must be constructed. All this, he said, is somewhat different from North America where the geog-

raphy is relatively simple.   It is indeed surprising to learn of this simplicity.   Schove presented a mean growth curve for Swedish Lapland and northern Norway with which he compared a graph of the mean temperature anomaly of the growing season, May–August, at Trondheim.   Analyzed, the graphs showed 74 parallel and 26 opposite trends.   In reference to distant correlations, Schove said that many attempts had been made but they have invariably proved unsuccessful, as is to be expected, because correlations between weather factors are also very small.

<div align="center">GROWTH AND RAINFALL</div>

By and large rainfall is the factor preferred in correlations with tree growth.   Rainfall records are rather widely gathered, apparently accurate in amounts, easily understood in a quantitative fashion, and easily adjusted for use.   Many points having to do with the selection of one factor as dominant in the growth picture have been mentioned before.   It seems necessary, however, to mention the work of Foster (1944) in the Middle West on the discontinuity in the areal correlation of annual precipitation.   He found high correlations over rather long distances in an east-west direction but low correlations north-south.   Dahms (1942) learned interesting information on the effect of weather conditions on chinch bug abundance in Oklahoma.   Light infestations occurred in years when the rainfall for the period from July 10 to August 20 of the preceding year was low.   Something of this nature in tree growth could give us false correlation with rainfall of the previous summer.

Not all workers have met with success in attempted tree growth-rainfall correlations.   Cook (1941b) found very little relation in eastern New York State.   In Wyoming Hansen (1940) studied spruce and fir on the east slope of the Medicine Bow Range.   No correlation existed between ring growth and annual precipitation at Laramie, 35 miles to the east and at a lower elevation.   In the north of Finland Hustich (1948a) reported little relation to rainfall.   At a distance of 130 miles between rainfall and tree growth correlations were: for June rainfall, $r = 0.08 \pm 0.17$; for July rainfall, $r = -0.24 \pm 0.16$; and for August rainfall, $r = -0.08 \pm 0.17$.   For trees and rainfall close together, r for June–September rainfall was -0.19 ± 0.13.   In northern Pennsylvania Meyer

(1941) obtained no significant correlation between growth and rainfall. In a letter to Glock dated April 7, 1942, Reed said: " So far as Iowa is concerned, I am inclined to believe that there is very little relationship between rainfall and tree rings ". Weck (1944) in central Europe apparently found no correlation between basal area increment and precipitation for the same year and poor correlation between increment and the precipitation for the preceding four years.

Many workers have found a rough, essentially qualitative relation between tree growth, as measured by width of annual ring on a cross section, and rainfall, measured at a gauge over different intervals of time. In a study on climatic changes Antevs (1948) pointed out that the usefulness of tree-ring records is limited because of the " fact that the radial growth of trees used is determined by the winter and spring (October–June) precipitation, little if at all by the summer rainfall . . .". The reason may be valid but the facts in the reason may not be so iron-clad. As it stands the statement is a trifle strong.

In 1923 Douglass reported agreement between tree growth and local rainfall at Prescott, Arizona, of 70 to 85 per cent, depending upon the use of a conservation factor. Little has been done in the 30 years since then to improve the amount of correlation or the methods employed. Perhaps restriction to the lower forest border which " separates the successful forest from the desert " (Douglass, 1931) has prevented not only improved results but also a better understanding of the course of growth.

In Australia Fielding and Millett (1941) reported that summer rains have an important influence on annual diameter growth.

The extensive work of Friesner in Indiana has emphasized the role of summer rainfall, although he recognized clearly that " The relation of growth curves to rainfall is not a simple one " (Friesner and Friesner, 1941). The highest percentage of correlation between 17 specimens of *Quercus borealis maxima* and rainfall existed for the period June–August, and these percentages varied from 48 to 74. Lowest correlation commonly was between growth and total annual rainfall. Six specimens of *Fraxinus americana* correlated highest with the same period as did the oak and lowest with annual rainfall. Correlation percentages with June–August rainfall varied from 61 to 77. By studying intervals

in which rainfall had increased over the previous year, Friesner and Friesner found that an increase of three inches in June brought a like response in 72 per cent of the cases, the highest of any interval.   When rainfall for November–October was ten inches less than the preceding year, the percentage of years with reduced growth was 82, the highest: " The important factor is whether the reduction in rainfall follows a year when rainfall was above normal or a year when it was about or below normal ". When individual trees agree among themselves from 90 to 100 per cent, growth and rainfall have similar trends.   Such trend correlation was perfect for June–August rainfall except for 1922, 1923 and 1931 (out of 1900–1939).   During these three years the rainfall of August–July gave perfect correlation.

In 1950 Friesner reported the trend agreement between growth and rainfall shown by six species of hardwoods from Indiana. The results paralleled to a great extent his former work.   On the whole the trend relationships were not high.   *Carya ovata* gave the highest agreement, 68 per cent, when compared with rainfall for May–July, but the range of agreement for 23 different rainfall periods was from 51 to 68 per cent, not drastically significant. *Carya glabra* ranged from 46 to 55 per cent for 23 periods.   Three periods, May–July, June–May and August–July, had 55 per cent. The results for four species were comparable with emphasis on the spring and summer rainfall.

Friesner and Friesner (1941) obtained like results with six species from Indiana.   Highest agreements were with growing-season rainfall and lowest as a rule with annual rainfall.   These results, favoring as they do the importance of growing-season rainfall, have particular significance because Indiana certainly can not be said to have a dry climate.

Glock (1950), working with conifers from near the forest interior of northern New Mexico, found greatest trend agreement (96.5 per cent) between growth and rainfall for March–July of 1909–1941.   This he said was " consistent with the principle of maximum correlation with minimum-length month-interval ".   The rainfall station was at a distance of five miles.   With a more distant and longer rainfall record he found higher agreement for the interval of 1898–1941 than for 1850–1897.   These results along with other criteria indicated a change in amount of rainfall or in its nature (see Leopold, 1951).

Hansen (1941) used the trend method of agreement in his work with three species of conifers from central Washington. The number of years of positive trends out of 36 were: with annual rainfall, all three species, 8; yellow pine, 14; western larch, 19; and Douglas-fir, 22; with March–August rainfall, all three species, 9; yellow pine, 11; western larch, 19; and Douglas-fir, 23. Certainly these agreements are none too high.

In the Mississippi Valley Hawley (1941) correlated pines with annual rainfall for a coefficient of 0.52, oaks with annual rainfall 0.33, and cedars with annual rainfall 0.65. The 23 pines used came from an area of many hundreds of square miles and were correlated with Cairo, Illinois, rainfall. Graphs were constructed (Glock, 1942b) for the purpose of deriving trends. For the years 1880–1930 there were 23 cases of parallel trend, 11 cases parallel but relationship slight, and 16 cases opposite trend. The same methods applied to 15 oaks gave 22 cases of parallel trend, six cases parallel but relationship slight, and 22 cases of opposite trend. " Cedar " growth compared with an unnamed rainfall station some 50 miles distant gave:

Calendar year

Growth vs. rainfall .... 14 parallel, 8 opposite
Growth vs. runoff .... 12 parallel, 10 opposite

Water year (November–October)

Growth vs. rainfall .... 13 parallel, 9 opposite
Growth vs. runoff .... 11 parallel, 11 opposite

These are poor relationships. As regards correlation coefficients given by Hawley, she said: " Correlations were computed for the 22 year period of 1911–1932, excluding the year 1920 in precipitation correlations, for which year the data are erratic ". If by chance 1920 was in high disagreement with growth then one is sceptical about its omission. We regret the absence of a complete explanation. A fuller review of Hawley's work is omitted here because it has appeared elsewhere (Glock, 1942a, b). However, one more point must be mentioned.

Miss Hawley tried to find homogeneous relationships over the vast territory of the Mississippi Valley. We are confronted with misgivings in the following: ". . . a lengthy drought indicated in the central Mississippi chronology must have been reflected in droughts on the Great Plains, although it is possible that on the

Plains the droughts may have been misplaced (*sic*) a year or so
. . . . The fact that the modern droughts of 1934 and 1936 were
so devastating in the Plains as well as in the central Mississippi
indicates that a very dry period is likely to cover both districts at
the same time . . .". Reference to the work of Hoyt (1938)
showed that Miss Hawley was right for 1936 and 1934 and also
for 1894, but partially or completely wrong for the remaining eight
out of 11 years of major drought. Thus there is grave danger in
drawing sweeping conclusions on meager data.

Huber (1941) constructed a rainfall calendar for pines in
central Europe and another one for fir and oak.

Lyon (1943) compared conifers with rainfall in the vicinity of
Boston. Hemlock correlated with May–July rainfall three miles
distant by 53 positive trends, 24 negative, and six with no trend.
On the whole the best correlations of pine and hemlock with rain-
fall were for the periods May–July and May–August. Lyon re-
ported his comparisons on the basis of wide and narrow rings; for
instance, in the case of hemlocks he used 52 out of a total of 81,
1856–1936. May–July rainfall thus showed 63.5 per cent positive,
13.5 per cent negative, and 23 per cent zero. Other rainfall in-
tervals were not so good. For white pine and May–July rainfall
the percentages were 63.3 positive, 22.3 negative, and 14.3 zero.
Lyon is fully aware of the complexity inherent in both tree growth
and rainfall. Secondary growth probably began in early May, and
hence "the most important and consistent control of the growth
increment is again shown to come through the growing season".

Miller (1950) in Indiana analyzed two species of *Quercus* and
one of *Fraxinus* in order to find what rainfall period showed the
highest correlation with growth and which portion of the trunk
gave the highest correlation. In all he used 23 rainfall periods of
various lengths from a station ten miles distant. *Quercus alba* gave
the highest trend coefficients with June–August rainfall, 75, and
with May–August, 71. When all rainfall changes up to 40 per cent
or greater were used, the coefficient rose to 83. *Q. velutina* gave
the highest trend coefficients with June–July, 70, and with June–
August, 70. *Fraxinus americana* gave the highest trend coeffi-
cients with May–August, 68, and with June–August, 60. In both
the oaks the top areas of the trunks gave higher growth-rainfall
trend coefficients than did the bottom areas: "This would appear

to indicate that annual growth in the top area of these species is more sensitive to rainfall changes than annual growth in the bottom areas ". Intra-specific correlations among the trees of *Fraxinus* averaged 77; among those of *Q. alba*, 79; and among those of *Q. velutina*, 72. Individuals agreed better within their own species, except for *Q. velutina* which agreed better with *Q. alba*. In all, trend correlations among trees, between tops and bottoms of trees, and between growth and rainfall, were of about the same quality. Growing season rainfall was apparently the important rainfall for tree growth.

Miller (1951) also studied nine sections of *Acer saccharum* from Indiana and compared them to rainfall records 13 miles distant. The highest trend coefficient, 63, was with June–July rainfall. With 63 per cent positive trend and 37 negative, tree growth and rainfall did not agree too well.

Schulman has done a great deal of work in the dry Southwest; one must not forget, however, in spite of the emphasis on dry climate, droughts and adverse conditions, that where trees grow there is enough water for them. It is, then, not so much a matter of quantity of water as it is a problem of when and how often soil moisture is available—if the trees are present. Too little water for a year or two, and the trees die. In the Southwest the correlation coefficient between seasonal rainfall and annual tree growth was about 0.6 (1940*b*) over an interval commonly of 50 years. It may even be 0.8 or more in some cases: " The indication of the dominance of precipitation on growth on dry sites of the Southwest is very strong ". In the present state of knowledge few would deny this, but, nevertheless, correlation coefficients, trend coefficients, visual comparisons, and above all an intimacy with the nature and processes of tree growth indicate clearly that rainfall, though of great import to tree growth, does not quite make that tree growth into natural rainfall gauges.

Since 1640 in the Southwest (Schulman, 1942*b*) four per cent of the years were characterized by extreme winter droughts with growth less than one-half of normal and about 15 per cent with less than three-quarters of normal. Summer rainfall had little effect. These may be important generalizations, especially if the annual increments were correctly determined in all cases. Another interesting point has been made by Schulman (1942*b*).

Trees under climatic stress of low rainfall may disagree with trees a few yards away not under stress, but they may closely parallel trees 400 miles distant.   In this connection it may be well to refer to the work of Pearson (1944a) who compared the ponderosa pines of Arizona and New Mexico: " New Mexico forests receive less winter moisture, more during May and June, and a somewhat lower annual total than do the Arizona forests.   The line of de-marcation does not conform absolutely to the State line but nearly so ".   Again Villeneuve (1946), remarking on climatic conditions in Quebec and their relationships to forests, said that a dry site tree in the north may be a wet site one in the south.   These cir-cumstances, in addition to what has been reviewed previously, are points of caution in long distance correlation.   Schulman himself (1942a) realized the nature of the problem in his work in Arkansas: " It is certain that local variations in both tree growth and rainfall introduce fictitious (sic) discrepancies in the pre-cipitation-growth relations . . .".   Of much interest was his in-formation that July–September rainfall was the most closely re-lated of seven intervals with latewood growth.   Occasionally en-tirely opposite trends were noted.

Weakely (1943) worked in western Nebraska where 80 per cent of the rainfall came April 1–September 30, with the greater part in April–June.   A dry mid-summer might produce double rings.   In spite of this distribution he correlated tree growth with annual rainfall.   North Platte tree growth correlated with North Platte rainfall gave $r = 0.63 \pm 0.05$ for ring widths and 0.73 ± 0.05 for cross-sectional area.   General tree growth correlated with general annual rainfall of the western part of the State gave co-efficients which varied from 0.51 to 0.54.   In some 400 years droughts average 12.85 years in length and no-droughts 20.58 years.

The results achieved during the past decade have been in general little or no better than those reported during the second decade past.   Correlations have been more widespread but not more fundamental.

GROWTH AND RUNOFF

Anything which contributes to our knowledge of variations in stream flow, although lacking high accuracy, can be of much utility to problems of power, irrigation and conservation.   In

recent years Schulman has worked diligently on collecting tree-ring samples to determine how well they represent stream runoff. Tree growth and rainfall are complex processes; runoff is no less complex.

In using runoff records for comparison with tree growth it must be assumed that there is a relationship between the soil moisture available to trees and the amount of water flowing past gauge stations in streams or that the two are influenced jointly by the same factor or set of factors. There is of course a relation between rainfall and soil moisture, and between rainfall and runoff. The complexities inherent in the rainfall–runoff relationship and in the rainfall–soil moisture–groundwater–runoff relationships are so great that it will be of interest to see what parallelism has been found to exist between tree growth and stream flow.

Lack of adequate knowledge of the entire province concerning runoff and the lack of space prohibit an exhaustive discussion. However, a few pertinent observations have come to our attention.

Cooperrider and Sykes (1938) have worked on the relation between rainfall and stream flow on the Salt River watershed above Roosevelt Dam in Arizona. The words of Cooperrider and Sykes, here applied to stream flow, sound very familiar from the growth and rainfall standpoint: ". . . the stream flow for any interval of time depends on many circumstances and factors and not alone on the amount of rainfall during the corresponding interval. Hence the extent to which any group of storms or the fall for some period contributes to stream flow is only vaguely revealed through general observations; neither is it definitely established through comparison of annual fall and flow records ". Runoff from melting of winter snow may be protracted well into the spring: " The beginning and ending dates of the annual rainy periods vary greatly ". In the summer, June–September, the storms are characterized by rainfall of high intensity. The two months of highest rainfall, July and August, contribute only slightly to stream flow, but that contribution is by means of direct surface runoff. In the winter, November–March, the storms are characterized by more general rainfall of low intensity. Its contribution to runoff is to a great extent through the groundwater percolation chain. April, May and October rainfalls are chiefly showers preceded and followed by dry weather; " they are ab-

sorbed by the dry ground and over a period of years contribute but little to stream flow ". When the percolation chain is well established, rainfall contributes heavily to stream flow. The base flow holds constant after the end of September and from then until January " there is almost no relation between rain and flow . . .". During the interval any changes are due to changes of temperature. Perhaps an excellent prerequisite to a study of tree growth and stream flow would be a thorough-going analysis of a drainage system similar to that made by Cooperrider and Sykes.

With some features of rainfall, percolation, and stream flow taken care of, Cooperrider and Sykes compared rainfall and stream flow. They reported a close relationship between average annual flow and winter rainfall during a 35-year period: ". . . the annual flow is more apt to agree with the winter than the average annual rainfall ". Therefore, if both tree growth and stream flow respond to winter rainfall, tree growth should equally correspond to stream flow. In contrast to the above quotation, Cooperrider and Sykes gave the following overall summary: " In general, the trend of annual stream flow may be said to follow closely the trend of annual rainfall. In fact, the relationship is close when one considers factors like *seasonal fall, flow lag,* and *fall distribution,* which may determine how large or small a part of a given annual fall is returned in flow during the same year ". The relationships are complex, a matter of which the writers of the quotations were well aware. Data of separate years showed mixture of lag and no lag. Rainfall distribution was complex. The year 1931 had the second highest fall in winter in 35 years, and yet annual flow was below average.

A comparison of rainfall and streamflow, 1902–1936, gave:

Annual trend . . . . 25 parallel, 9 opposite
Summer trend . . . . 27 parallel, 7 opposite
Winter trend . . . . 22 parallel, 12 opposite

Two of the 25 parallel, above, showed no change in rainfall from one year to the next, but showed a large change in flow; one of the 22 parallel showed the same change. The figures of trend given above, between rainfall and stream flow, are not too encouraging. Now we may report correlation coefficients given by Cooperrider and Sykes:

Annual flow vs. rainfall 0.79
Summer flow vs. rainfall 0.67
Winter flow vs. rainfall 0.81

Graphs showing accumulated excess and deficiency of rainfall and stream flow for the upper Salt River watershed gave 24 parallel, ten opposite. Another method of analysis was to examine the averages: 19 out of 35 winter rainfalls were above average, 16 were below. Ten of those having above-average rainfall also had above-average annual flow; 14 of the 16 with below-average rainfall also had below-average flow. It may be well to summarize the above matter in the words of Cooperrider and Sykes: " The ratio of stream flow to precipitation is never a constant, the amount of precipitation being only one of the factors affecting annual stream flow ". Over the drainage basin as a whole the total rainfall, 1902–1936, was 711 inches; total stream flow was 116 inches. Hence, 16.3 per cent of the rainfall was returned as stream flow. The right kind of rains may keep soil moisture high and yet give little to stream flow. One can conclude only that the subject of stream-flow relationships contains many phases and that it is indeed complex.

Croft (1946) analyzed water-supply factors in the inter-mountain area, and stressed mantle-moisture content. A wét soil increases runoff. In contrast, " Rainfall is not effective in producing stream flow, except as channel interception, after the soil mantle attains a definite capillary moisture deficit near the surface ".

Hansen (1940) was interested in growth and dominance in a spruce-fir association in the Medicine Bow Range of Wyoming but, none the less, gave consideration to runoff: " Most of the precipitation in the spruce-fir forest occurs as snow, and the amount of moisture lost through runoff and evaporation is not necessarily a function of the annual precipitation ".

Hoyt and Langbein (1944) have given us much information on the relationships of stream flow to different climatic factors. They announced at the start that " Stream flow is dominantly the integrated result of many diverse climatic factors ". Also, it is influenced by soil, rock, topography and other factors: " Stream flow has its origin in precipitation, but the portion that will drain from the land to the streams is conditioned by complex inter-relationships still only imperfectly understood ". In addition to

such general statements, Hoyt and Langbein gave analyses of temperature effects and of the areal extent of excessive and deficient stream flow by years. This information is highly significant indeed in relation to correlations of tree growth over long distances. Stream flow is a natural measure of the net amount of water that escapes evaporation and transpiration: " Precipitation, representing the supply, is . . . fundamental, but its time distribution and influences of other climatic factors may substantially modify its effects ". Surely we must be able to cope with all the intricacies of soil moisture, groundwater hydrology and runoff before we can understand the devious course taken by the chain of relationships between tree growth and runoff.

A report by the Regional Forester (1951) for the Arizona-New Mexico region gave data on stream flow in three small mountain water sheds in central Arizona. Results corroborated those obtained by Cooperrider and Sykes in that the percentage of summer rainfall appearing as stream flow varied from 2.1 to 3.8 for the three watersheds, whereas the percentage of winter rainfall varied from 14.7 to 31.6. Little summer rainfall appeared in the streams.

Schiff (1951) also worked with small watersheds. At times more rainfall gave less runoff.

Thornthwaite (1945a) studied rainfall and runoff of the James River basin and the Great Valley of Virginia over a period of 31 to 37 years. Trend analyses were made of rainfall and runoff in the two regions. For the Great Valley there were 29 parallel, seven opposite trends; for the James River 22 parallel, eight opposite. A comparison of the rainfall of the two regions gave 27 parallel, three opposite; of the runoff 31 parallel, five opposite. The trends of the data for combined rainfall and runoff gave 20 parallel, ten opposite. Trend reaction for the two basins, regardless of the nature of the trend, gave 23 parallel, seven opposite. One can see the operation of factors other than rainfall in these comparisons.

With the above all too brief discussion of the complexity in runoff relationships we must pass on to some of the results obtained by attempts to correlate tree growth and runoff.

In 1941 Hawley compared " cedar " growth and runoff of the Norris Basin, and obtained $r = 0.61$ for annual rainfall and $r =$

0.56 for the water year of October–September. Search of the written report failed to disclose the location of the " cedars " and the particular stream whose flow was used as a measure of runoff. Because the graphs of the report are in a very unsatisfactory condition no separate analysis is here attempted.

In 1945 Schulman (1945c) reported a preliminary study of tree rings as an index of runoff on the headwaters of the South Platte River.

Schulman (1945a) reported rather extensively on tree growth and runoff of the Pacific slope. A complete reading of his work leaves an impression of over-simplification, although, if he had paid attention to all factors, his exploratory work would have been greatly increased. Exploratory work is necessary, perhaps to be performed even before the fundamental course of growth is understood.

Schulman gave graphs and data which included October–June rainfall at Durango, Colorado, Animas River runoff at Durango, Mesa Verde tree growth (seven trees), Rio Grande runoff near Del Norte, Colorado, and tree growth (one tree) at Wagon Wheel Gap, Colorado. Schulman gave correlation coefficients; the present writer made trend analyses of the graphs. Tabulated results give:

1. Durango rainfall vs. Animas River runoff—34 parallel, 6 opposite
2. Mesa Verde growth vs. Wagon Wheel Gap growth—63 parallel, 28 opposite
3. Durango rainfall vs. Mesa Verde growth—36 parallel, 11 opposite
4. Animas River runoff vs. Mesa Verde growth—30 parallel, 10 opposite
5. Rio Grande runoff vs. Wagon Wheel Gap growth—39 parallel, 12 opposite
6. Animas River runoff vs. Rio Grande runoff—33 parallel, 6 opposite

$$\text{For No. 3 above: } r = 0.78$$
$$\text{For No. 4 above: } r = 0.73$$

In relation to No. 1, Schulman said that rainfall was " obviously paralleled " by runoff. In relation to Nos. 3 and 4 he said that tree growth gave a " reasonably close index " of both rainfall and runoff. Because the two drainage basins are close together, " the chronology in tree growth (No. 2) and in runoff of the two areas (No. 6) is essentially identical ". There is considerable latitude in the near identity.

There are many difficulties in the use of station rainfall records and gauge records of runoff when those records are distant from

the trees. We are faced with these disadvantages over much of the forested area, and Schulman (1945a) had to work against long distances. It is difficult to reconcile his statement: "The generally parallel march of fluctuations in precipitation at San Francisco and San Diego . . . indicates a general tendency to uniformity in annual chronology along some 500 miles of coast southward from San Francisco " with a trend analysis which gave 63 parallel and 29 opposite. Correlation of San Jacinto district tree growth with San Diego rainfall gave $r = 0.44$ and a trend analysis of 67 parallel, 24 opposite. The same tree growth correlated with Kings River runoff gave $r = 0.59$ and trend analysis of 24 parallel, 22 opposite; with San Gabriel runoff, $r = 0.57$, trend analysis gave 31 parallel, 15 opposite. Schulman fully realized the " dubious value " of such distant comparisons.

In his work on tree growth of the Colorado River basin Schulman (1945b) discussed the necessity of very particular methods of field selection of trees. He said: " Experience has shown the possibility of ' improvement of the data ' by the repeated refining of field sampling criteria; this is a magnificent property of tree-ring indices, which in a very basic way cuts the Gordian knot of errors in the relationship of these indices to rainfall and runoff ". This statement could be considered somewhat extravagant when it is compared to the change which has occurred from a previous statement (1941) which said: " Criteria for selection are based largely on common sense, plus a generous dose of practical experience ".

Schulman took cores extensively over the West, including trees from the Green River basin, Colorado basin above the Gunnison, Gunnison River basin, Dolores River basin, San Juan River basin, Southern Utah, Salt River basin, Gila River basin, and southern Arizona. This was a tremendous project and should give a fairly good idea of the agreement not only between tree growth and runoff but also between tree growth and such rainfall stations as were available. The records of eight streams from British Columbia to southern Colorado were given; they ranged in length from 1890 to 1941 and 1911 to 1941. If all are compared regardless of length it is found that nine out of 51 agree in trend. For the North Platte, Colorado, and the Rio Grande, 20 out of 30 agree.

Results are none too encouraging among the tributary basins of

the Colorado system. Only a sample tributary will be given, the Green River basin. Two rainfall records, October–June, gave 20 parallel, ten opposite trends. Runoff compared with tree growth gave 19 parallel, 15 opposite. Tree growth compared with one rainfall record gave 16 parallel, 14 opposite, and with the other rainfall record 23 parallel, 17 opposite. This second rainfall record compared with runoff gave 23 parallel, 11 opposite. Five other tributaries showed comparable results. Concerning these comparisons Schulman said: " In spite of the obvious general parallelism in the rainfall-growth comparisons . . . , there are evident in almost all some apparent disagreements between the fluctuations in growth and those in recorded winter precipitation ". No significant relation between summer rainfall and growth was noted and, further, there was no unqualified effect of summer rainfall on next year's growth. In all tributary basins Schulman found a " fair degree of correspondence " between tree growth and rainfall and between tree growth and runoff.

Southern California was given critical attention by Schulman (1947). A general parallelism was found in the seasonal rainfall over much of south and central California. A trend analysis of the seven stations recorded gave 11 parallel, 19 opposite. Comparison of each two stations gave trends ranging from 26 parallel, four opposite, to 19 parallel, 11 opposite. In the Coast Range tree growth versus rainfall gave $r = 0.65$, or in trends 29 parallel, 11 opposite. Tree growth versus southern Sierra rainfall gave $r = 0.58$, or in trends 28 parallel, 12 opposite. Tree growth versus San Gabriel River runoff gave $r = 0.61$, or in trends 28 parallel, 12 opposite. Tree growth versus Kings River runoff gave $r = 0.52$, or in trends 27 parallel, 13 opposite. Rainfall of the southern Sierra versus Kings River runoff gave 30 parallel and ten opposite trends. These figures are as significant for a comparison of the correlation coefficient with trend analysis as they are for the degree of agreement between tree growth and rainfall and between tree growth and runoff.

Schulman (1947) also gave inter-regional correlations but their significance does not justify extended discussion here.

In the Navajo National Monument Schulman's work (1948a) produced a growth record extending back to 698 A.D. Tree growth appeared to reflect the winter rainfall.

In a summary of his tree-ring work, Schulman (1951) correlated regional tree-ring indices with rainfall and runoff. Tree growth in each case which follows was correlated with the rainfall or runoff indicated. Colorado River basin: Colorado River runoff, October–September, $r = 0.66$; Eastern Oregon: Eastern Oregon rainfall, September–August, $r = 0.50$; Columbia River runoff, January–December, $r = 0.56$; Southern California: Coastal rainfall, July–June, $r = 0.65$; Kings River runoff, October–September, $r = 0.52$; San Gabriel River runoff, October–September, $r = 0.61$. Do these coefficients give us any direct information on the chances of parallel variation in any one year between tree growth and either rainfall or runoff?

Schulman (1951–52a) extended his activities to Big Bend National Park, Texas, where the available rainfall record lay 250 miles away at El Paso. Tree growth, he said, " tends to parallel " the march of winter rainfall. Trend analysis gave 39 parallel, 21 opposite, between tree growth and October–June rainfall. Perhaps the Big Bend trees " provide a better index of local rainfall than is evident " from the graphs because " the distance factor acts strongly in this region of variable and spotty rainfall ". A collection was also obtained from the Guadaloupe Mountains 200 miles north-northwest of the Big Bend, and the growth record there closely paralleled tree growth from the Big Bend. Analysis showed 65 parallel, 25 opposite trends. A comparison of Guadaloupe tree growth with Carlsbad, New Mexico, October–June rainfall, gave 24 parallel, 16 opposite trends. Tree growth versus Pecos River runoff gave 21 parallel, nine opposite trends. Carlsbad rainfall versus Pecos runoff gave 18 parallel, 12 opposite trends. It seems clear that these figures do not show a strong parallelism.

In a progress report Schulman (1951–52b) adopts two innovations. The first and more important was the extension of the growth-rainfall relationship to the rainfall of July–June from that previously employed, the winter rainfall of October–June. Naturally such a relation would satisfy our fondest hopes—that tree growth records annual rainfall rather than that of the growing season. Perhaps, however, it is asking a great deal of trees to record moisture that passes through the soil when they do not use it actively. An intense desire to find an index of annual rain-

fall should obscure neither the quality of the evidence nor the methods whereby that evidence is obtained.

The scond innovation was the adoption of a coefficient of sensitivity. In 1928 Douglass defined mean sensitivity " as the difference between each two successive rings divided by their mean ". It gives in essence the degree of variability in a sequence and as such has high value in giving the fluctuations and inter-relations of growth-factor influences whatever they may be. Of all devices that give an insight into the vicissitudes of tree history, mean sensitivity seems to be the most revealing. Schulman has based his coefficient on mean sensitivity. This coefficient, R, is the ratio of group sensitivity to the average of single tree sensitivities. As we understand it, group sensitivity is the mean sensitivity of the merged growth record; the other part of the ratio is the average of the mean sensitivities of the trees taken singly. Thus, there is a re-use of data and trees are compared with themselves by a rearrangement of the figures representing their sensitivities. Does R have a functional value? What is its advantage over the mean sensitivity of Douglass? Schulman's data show an increase in the value of R with approach to the desert border. The drier the site (and the more violent the fluctuations in certain growth factors) is, the higher the value of R. But this is also what mean sensitivity shows (Douglass, 1928; Glock, 1937).

Schulman (1951–52b) asserted that a single radius often gave a remarkably faithful record of rainfall and runoff. One tree from Mesa Verde compared with Rio Grande runoff 100 miles distant gave $r = 0.68$; a second tree gave $r = 0.65$; and the average of the two trees versus runoff gave $r = 0.72$. Averaging apparently has the same effect as smoothing. One tree from near Pecos, New Mexico, compared with runoff of the Pecos River, and some 12 miles distant " from the weighted center of rainfall in that basin above the tree site ", gave $r = 0.78$; a second gave $r = 0.49$; and the average of the two trees gave $r = 0.72$. Aside from the questionable practice of using the correlation coefficient in continuous time series, what is obtained by such a coefficient? It means no doubt a certain amount of covariation during certain years. But it also means that in certain years tree growth varies in the same direction as the runoff: that runoff consisting of rainfall past and present which the trees did not and could not use.

Tree growth is compared with something that does not affect it, a rather round-about method. This does not mean to say that we should not grasp the opportunity of employing tree growth to reveal runoff if we can. Weakness must be recognized as well as strength. In the evidence presented runoff does not parallel tree growth year by year for all years; thus we obtain a general picture, not a detailed one. In reference to the four trees above mentioned Schulman (1951–52b) said: "These specimens are indeed highly selected; however, it is estimated that at least 20% of the trees under analysis have this order of fidelity to the appropriate rainfall and runoff series". The other 80 per cent, presumably, do not measure up to the quality or coefficient value of the 20 per cent, and that is subsequent to field selection. In the introductory paragraphs (1951–52b) Schulman remarked that he had begun work of a nature "to develop more secure interpretations of the ring records in terms of absolute values of past rainfall and river flow . . .". The results so far represent an enormous amount of work but are as yet not too encouraging in terms of the ultimate objective.

GROWTH RINGS AS A TOOL

Growth rings are not always used as attempted substitutes for gauges of rainfall or temperature or runoff. They have given the dates of certain events, and, because of the value of the method especially as developed in recent years by Lawrence, brief mention will be made of the work more as a matter of reference than as an exhaustive discussion.

The age of stands affected by glaciers, the time of ice advance, and the time of retreat have been closely approximated by counting the growth rings of the proper trees (Butters, 1914; Cooper, 1923, 1939; Lawrence, 1950; Lawrence and Lawrence, 1949; Mathews, 1951; Nichols and Miller, 1951; Sharp, 1951). Langenheim (1949) dated landslides in Colorado by means of the eccentric rings in trees tilted by the slides. In Texas, Roth (1945) counted the rings in trees perched on small erosion remnants in order to obtain the limits within which the last epicycle of erosion began. Hansen (1946) referred to charcoal logs buried by pumice from Mount Mazama; they suggested that the climate at the time of the eruption was similar to that of today.

CONCLUSION

A review and analysis of all material pertinent to tree growth are tasks of such magnitude that years of work would be required for their accomplishment. Without doubt important studies have been omitted unintentionally.

How well we have analyzed trends as listed in the Introduction the reader must judge. Two main points stand out: a) Investigation into the fundamentals of plant growth; b) attempts to use growth rings as natural gauges of temperature, rainfall or runoff. Much work yet to be done separates the two. In reference to the use of tree rings, Dobbs (1951) has said that " At present the only undeniable record of climatic effect upon the wood is the frost rings . . .". Even so, " It can scarcely be overemphasized that the whole history of a tree's growth in relation to its environment is recorded in its wood, and that it needs only the separation of the general from the special elements in that record to make it intelligible " (Dobbs, 1942). Fundamental work is never ended, and in reference to tree growth " extensive experimental studies under controlled conditions are desirable at the outset " (Sampson and Glock, 1942) and are as important today as they were ten years ago. If a review of the literature has given us one primary impression it is to the effect that tree growth will eventually be understood by an approach through plant physiology and anatomy, and conditioned by a knowledge of growth factors, internal as well as external.

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THE BOTANICAL REVIEW

DISINFESTATION OF SOIL BY HEAT, FLOODING AND FUMIGATION

A. G. NEWHALL [1]

INTRODUCTION

Will the capacity of our agricultural lands to produce sufficient food keep pace with our ever-growing population? Now that the frontiers have been pushed across the American continents, this Malthusian spectre is again raising its ugly head. An increase in population of approximately one per cent a year can not possibly be matched by a like increase in available new land during the next century or two, and what is brought under cultivation will be at

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ever increasing cost and of lower productivity. A considerable amount of good land is being taken out of production by the growth of cities, paved roads, airports and parking areas. The need for increasing yields and avoiding all possible losses on crop land still available is obviously of increasing importance. The more obvious insects and diseases operating above ground have received much attention, to the great benefit of agriculture, but the more obscure ones operating below ground have not been accorded the study they deserve. A review of soil sterilization and fumigation will indicate how far we have come and perhaps suggest future trends. The present discussion is arbitrarily limited to flooding and to materials and methods involving heat and volatile chemicals which disinfest soils. Chemicals which act primarily as protectants, inhibitors or repellants are excluded, since they are regarded as soil amendments, as described by Daines (1946). The line is hard to draw and complete agreement is not expected.

APPLICATION OF HEAT, AND THERMAL DEATH POINTS OF PATHOGENS

The value and simplicity of heat treatments derive from the fact that most soil-harbored plant pathogens, as well as weed seeds, have rather low thermal death points. This includes insect pests, nematodes and even many of the viruses which have inactivation temperatures below 80° C. One exception is tobacco mosaic virus which requires 92° C for ten minutes, according to Johnson (1946); another is the chrysanthemum stunt virus which will stand boiling (Brierley, 1952). The relation between duration of heat (X) and the thermal deathpoint (y) is fairly well expressed by a curve of the general form $(y - a)\sqrt{X} = b$, according to van Koot and Wiertz (1947) who found 50° C to 70° C adequate for certain Verticillia and Fusaria.

It seems likely that thermal death points in many instances are merely protein-coagulating or enzyme-inactivating temperatures. Albumens and glutamens are notably not heat-stable. Work on thermal death points has been summarized by Elliott (1930) for bacterial plant pathogens, by Newhall (1940) for a number of fungi and nematodes; and others have pointed out that pasteurizing temperatures are adequate for specific pathogens (Horsfall, 1935; Vladimirskaya, 1930; Milbrath, 1929; Pittman, 1931; Grooshevov

et al., 1940; Williams et al., 1943; Van der Want, 1948; Togashi, 1949).

Nine-tenths of the sunshine reaching the earth is absorbed as heat. According to Harrison (1944), this amount is equivalent to the energy in nearly one-half pound of coal, or about 6000 B.T.U.'s per square foot per day. That this amount of heat is actually enough to effect partial sterilization of the surface soil is entirely possible for some soils in parts of India during April and May, according to Burgess (1929). Hoshino and Godfrey (1933), in a review of the temperature relations of *Heterodera radicicola*, state that soil temperatures may go high enough to kill the larvae of this nematode to a depth of three inches at times in parts of Texas. Thus plowing three times at seven- to ten-day intervals during hot weather has been suggested as a means of control for this pest. This is effective also in the Coachella Valley of southern California where it permits a fairly clean crop of carrots to be grown, in otherwise nematode-infested soil, during at least part of the year.

The repeated observations by our early settlers that the locale of brush fires was always the best place to plant tender crops and to build seedbeds have repeatedly been confirmed by scientific investigation. Burgess (1929) states that crops are far superior in England where couch fires are started in the spring, and his tests showed that top temperatures of 63° to 82° C might be reached at a depth of four inches in such areas. Kelley and McGeorge found similar temperatures in Hawaii (1913). Kletschetoff (1930) reported observing fair control of flax sickness, due to an accumulation of fungi in the soil, in parts of Russia where vegetation in the fields was burned off before sowing. Chowdhury (1944, 1945) and Reitsma and Sloof (1950) advocate control of diseases of pan in India by burning rice straw or thatching grass over the soil repeatedly until a temperature of 60° to 65° C is reached in the first nine inches of the soil, a process requiring turning the soil and burning as many as four times. Chowdhury also recommends heating soil directly, with a flame gun (2000° F) to 75° to 82° C for a depth of six inches for control of *Sclerotium rolfsii*. Tea plants on the island of Bali today are commonly set in

soil at points where bonfires of soil and sawdust have been built (Gerald Thorne, personal communication).

Surface burning and roasting have been practiced most extensively in the burley tobacco-growing areas of the southern United States where it has been in vogue for at least 60 years to control Thielavia root rot and weed seeds. The practice spread to Italy, West Australia, South Africa, France and Yugoslavia. (Benincasa, 1902, 1907; Peglion, 1900; Cappelluti, 1902; Wuiovich, 1907; Gilbert, 1909; Scherffires, Wooley and Mahan, 1909; Scherffires and Taylor, 1911; Beinhart, 1918; Clayton and McMurtrey, 1950; Loeters and Stam, 1952).

There are over a million acres of burley tobacco grown in the United States, which, at 600 to 900 square feet of seedbed to the acre, requires 14,000 to 20,000 acres of seedbed. If these beds had to be doubled in size to get enough good plants, the cost is estimated at $4 million; so bed treatments are cheaper. When seedbeds were nestled in clearings in the woods, there was always ample brush and slashing to burn, but as woodlands became less abundant, particularly in the more northerly States, more convenient though costlier methods of eliminating weed seeds and root rots were developed. Control of root rot became more important as permanent seedbeds became more popular and rotation less common. Comparisons between surface burning or direct roasting, indirect roasting or pan firing, in which the soil is shovelled into a pan over a fire, and other treatment, such as the formaldehyde drench, various steaming devices and the use of boiling water, have shown that, in general, steaming and roasting give better results than hot water, formaldehyde or surface burning. The Wyatt tobacco bed burner, or soil roaster, on a pair of wheels is capable of treating 100 square yards a day, according to Clayton and McMurtrey (1950). These seedbed treatments are carried on between November and March. The extent to which market gardeners have gone to insure disease-free soil for potting plants and seedlings is well illustrated in the description of the Warburton, the Shewell-Cooper (1937) and numerous other vertical and horizontal ovens for roasting or baking soil over coke or coal in England (Bewley, 1926, 1929).

An interesting variation of the soil roaster was built by Viscount Elveden (1921) who heated soils in various ways. One of

these was by flaming it in a rotating drum which heated about a ton an hour to a temperature of 80° C. A similar device has recently been shown by Newhall and Schroeder (1951) to be practical in the continuous pasteurization of compost soil at the rate of two cubic yards an hour with the use of but 60 cents worth of kerosene fuel. The device is an adaptation of an aggregate heater used in road repair work and is marketed in the United States for both purposes.

In all of the roasting and direct firing methods, the presence of moisture in the soil is evidently the safeguarding factor in preventing overheating and destruction of organic matter. That some injury may be expected from the prolonged treatment recommended in England is admitted by Bewley (1947, 1950) and by others who have advocated either wetting the soil a few hours after treatment or treating soil several weeks before trying to grow plants in it. Knowledge of thermal death points and development of speedier methods of heating soils have eliminated much of the dangers from overheating. Nevertheless, where steam is available it has tended to replace roasting methods.

STEAM HEAT

Methods of applying steam were brought to their present state of efficiency chiefly by vegetable and flower growers, largely in America, in England and in Germany. The scientists, with few exceptions, observed what was going on, devised experiments for explaining the phenomenal results obtained, refined procedures, and, of course, disseminated the information. For his work in the last field, he has received a disproportionate share of the credit due many ingenious practical growers who were driven to do something to reduce losses from disease organisms, chiefly nematodes, in their soils. Steaming has two great advantages over all other methods; being non-selective, it gets all pests, and it leaves the soil quickly with no trace of harmful residue. The benefits in better growth are often noticed to last for several succeeding crops.

The early use of steam in combating root knot has been reviewed by Stone and Smith (1898). They may be looked upon as the fathers of practical steam sterilization of greenhouse soils in America. Since then a number of different methods have been

developed. Small quantities of soil have been steamed in a shallow bin with perforated pipes laid in the bottom ever since it was first described by May (1898). Steam chests of wood, concrete, brick or cast iron have all been constructed, even canners' pressure cookers have been employed. Popular models in England have been described by Falconer (1928), Hinks (1932), Lawrence and Newell (1938) and Bewley (1929), and in the United States by Newhall (1930), Fosler (1950), Ball (1950, 1952) and Steven (1953).

With all of these steam bins, the soil has to be brought to the steaming device and carted back again after it is heated, which involves time and much labor, although of late the use of power-driven, tractor-mounted, soil-moving equipment has greatly reduced both. Growers early devised ways of bringing steam to the soil, especially to ground beds to be treated for nematode control. This step, first announced by Selby (1906), doubtless was taken by many growers independently, perhaps before that time.

INVERTED PAN OR TRAY. For seedbeds and soil in shallow benches or even ground beds, a metal pan inverted and weighted down, under which steam is admitted for a period of 20 to 50 minutes, has served well at low cost for materials. Probably this was first used by the Wutrick Brothers in about 1895, and definitely was used by Bolley (1913) in 1911, who pictured it beside a portable steam boiler in North Dakota grain fields. It was formally described by Beinhart (1918), Selby and Humbert (1915), and more recently by Sackett (1927), Magee (1931) and Bewley et al. (1947). A variety of labor-saving devices to aid in the moving of the larger sized ones have been invented (Newhall, 1930; Newhall, Chupp and Guterman, 1942).

The latest substitute for a metal pan, described by Dimock and Post (1944) as a surface method of steaming benches, employs a rubberized cloth or stout kraft building paper or plastic tarpaulin, the edges of which are held down by weights while steam is directed between soil and cover. Where soil has been thoroughly loosened and steam pressure is below 15 lbs., such light weight covering is satisfactory and economical. The method demonstrates clearly that steam does not have to be driven into soil under great pressure but merely has to be exposed to the soil to effectively heat it. Deep penetration of heat below six inches does not take place

readily under the pan or surface method because the upper layers of soil become saturated, thus hindering further ingress. The method is better suited to bench than to ground beds.

Some ingenious ways of cutting down on the labor and equipment required to steam by the surface method have been described by Ball (1953a). They include the use of canvas hose laid on the soil surface in place of metal pipes as steam-conductor and a wooden frame covered with plastic tarp built over this hose, all of which together can be pulled by ropes to the next position every two or three hours without turning off the steam or walking on treated soil.

BURIED PERFORATED PIPE OR GRID. This method, first described by Selby (1906), was called the " ordinary greenhouse method " by Gilbert (1909), so general was its use in Ohio by then. It consisted of a series of pipes, usually one inch and perforated at one-foot intervals, laid in parallel trenches about a foot deep and 15 inches apart, through which steam was passed until the entire soil mass above was heated to 210°. There are many variations as to number, length and depth of pipes served by one steam header. It has been widely used in Europe and America. Its advantages lie in the thoroughness and depth of heating achieved. Bewley states that one year in four may be often enough to steam by this method in holding down root knot. Its disadvantage lies in the labor of burial and relocation every hour or so (Sackett, 1927; Newhall, 1930; Bewley, 1923, 1926, 1929, 1947, 1950). Smaller models have been placed in dump trucks or tip carts, and even wheelbarrows (Schwartz, 1933; Quantz, 1937; Roll-Hansen, 1949).

SPIKE, STEAM HARROW OR RAKE. This device consists of a grid of pipes with hollow pointed spikes at right angles to it, like a six-foot long hair-brush. The spikes, six or eight inches apart, are pushed into the ground, and the steam, led to it through a flexible hose, is turned on for 15 to 30 minutes at a time. Tests in Ohio by Newhall (1930) indicated it to be a cheap device for getting shallow or superficial jobs of heating done. The method has been discontinued in America. But Cunningham (1938) in Australia combined the features of a harrow with a pan and obtained pasteurization temperatures to a remarkable depth, 14 inches, in a minimum

of time, seven to ten minutes. It requires considerable labor and is slow.

BURIED TILE. Galloway, according to Stone and Smith (1898), was the first man to employ two-inch, porous, clay tile to conduct steam into a bin holding 72 cubic feet of soil to control soil pathogens. Stone and Smith (1898) showed how far apart the tile lines could be set. Their work laid the foundation for practical application of steam to greenhouse ground beds for the next half century. Their temporary system has given way to a permanent layout which is often put in before a greenhouse is built, at which time ditch-digging, tile-laying machinery can be used to advantage. Various layouts have been described (Brown, Baldwin and Connor, 1922; Brown, 1926; Newhall, 1930). The optimum depths and spacing of tile lines were found in Ohio to be 18 inches apart and 19 inches deep. Brown found lines three feet apart inadequate to control *Fusarium* wilt of tomato. One large grower in Ohio found lines two feet apart unsatisfactory and reset them all 18 inches. Lines 22 inches apart and only six inches deep sometimes failed to control tomato wilt at the Ohio Experiment Station. Steam has been successfully used in beds 40 feet wide, fed through only one header. Likewise lines as long as 110 feet have been steamed from one end with one or more boilers of 100 horsepower. Tile lines have been in annual use for as long as 27 years before being dug up and reset.

Areas of ground beds successfully steamed per boiler horsepower vary a good deal. With the shallower harrow and pan methods, up to three and one-half square feet were commonly treated, and the time to treat a unit area was less than an hour. With methods that steam soils more deeply, as buried pipe and tile, from six to eight square feet may be steamed per horsepower without waste, though much longer times per unit area treated are required. In several greenhouses 12 square feet per boiler horsepower have been steamed, and one or two have done 24 to 26 square feet, but such areas require from 10 to 24 hours of continuous steaming, and when a few tile are clogged, it may take many wasteful hours to find it out. From an economic standpoint, the best system is the one that forces the largest number of B.T.U.'s into the soil in the shortest time with the least labor. In Europe, where labor costs have been comparatively low, the tile method has not looked at-

tractive until recently on account of its high initial cost, but in America it has paid in the long run to put the money into such equipment lasting 20 to 30 years rather than into as many annual labor charges.

CONDITIONS CONDUCIVE TO EFFICIENT STEAMING. All workers agree that soil should be loose, free from lumps and preferably on the dry side in steaming operations. Steam flows through the paths of least resistance. As pointed out by Russell and Pethybridge (1912), water requires four times the number of B.T.U.'s that sand or clay does to raise it one degree F, since the specific heat of dry soil is only .23. So a soil with 60 per cent moisture requires two times the heat units that one of 20 per cent needs. They conclude that, if one could get 100 per cent efficiency, a pound of coal containing 12,000 calories should heat from 100 to 340 pounds of soil from 52° to 212° F. But in practice such an amount of coal heats only 30 to 100 pounds of soil; and to raise a ton of soil to 180° F requires about 50 pounds of coal, so one gets only about 30 per cent efficiency. If a pound of coal potentially should heat 100 pounds of soil from 52° to 212°, and if a six-inch acre weighs two million pounds or a thousand tons, it should take about 13 tons of coal to steam an acre one foot deep. Assuming 30 per cent efficiency, it would actually take over 40 tons of coal. This is roughly what many greenhouse tomato growers in northern Ohio used, according to Newhall (1930) and Senner (1934). Roll-Hansen (1949) gives the specific heat of soil at 0.5, which means that 500 kilo-calories are required per cubic meter per degree rise. Since one kilo of steam is good for 600 kilo-calories, it requires 75 kilo-grams of steam to heat one cubic meter of soil to 90° C. Under ordinary good conditions, he states that about 60 per cent efficiency is achieved today.

Bewley with tray or inverted pan used 3200 pounds of fuel to treat 2160 square feet to a depth of 12 inches, which is one and one-half pounds of coke per cubic foot of soil treated or 32.6 tons per acre. In another test he used two pounds of coal per square foot with both the buried tile and the inverted pan methods or 43 tons per acre, and he gives nine square feet and three square feet as the amounts one can expect to do per boiler horsepower, respectively. It seems that from two to four cubic feet of soil an hour per boiler horsepower, no matter what method is employed,

is what one should be able to steam, depending upon soil moisture, original temperature, size of conductor, distance from the boiler and firing efficiency.

A few items contributing to the maximum efficiency of the steaming method would be withholding moisture from the soil for a month prior to treatment, insulation of the pipes from boiler to site of steaming as advocated by Bewley, a water trap to collect condensate before it enters the soil, and a pressure gauge at the site of steaming rather than on the boiler, as advocated by Brown, Baldwin and Connor (1922). Brown (1926) points out that it is the volume of heat units passing into the soil that counts and not just the boiler pressure, which makes size of pipes of great importance. Ball (1952) stresses adequate sized conductor pipes, particularly where low pressure steam is employed. Newhall, Chupp and Guterman (1940) give tables to show the amount of steam carried by pipes of various sizes under various pressures, together with the line drop or loss with distance from the boiler.

No one stresses the need for high pressure steam any more; in fact, many hot water-heating plants have been converted by florists to low pressure steam generators in the last ten years for soil-steaming purposes, with almost universal satisfaction (Ives and Ives, 1953). The pressures are from five to 15 pounds per square inch. The Thomas surface method of steaming works well on low pressures. Almost no pressure was employed in the Moore copper kettle method, described by Bewley (1923), or in the electric pan steamer, described by Newhall (1940). Scheffer (1930) employed but six to eight pounds pressure with apparent success. Senner (1934) concluded that a final soil temperature of 212° F is all that can be obtained, regardless of initial steam temperature or boiler pressure. High boiler pressures did not materially lower the total steam required nor did they greatly affect the amount of water which normally accumulated in steamed soil. He believed the so-called merits of high pressures were largely mythical. Jacks (1953) found high and low pressures to give equal results. However, Bewley (1926) and Hunt et al. (1925) both found with the inverted pan that doubling the steam pressure almost doubled the rate of heat penetration into the soil. Perhaps the same could have been obtained by an increase in the size of the steam conductor pipes.

Addition of formaldehyde to the soil to be steamed or its introduction into the steam line during the process has been tried by Winston (1913), by Beachley (1937) and by Manns (1947). It is said to reduce the time required to steam a unit area and to increase the efficiency of low temperature heating, but Hunt et al. (1925) got no appreciable benefits from the addition of formaldehyde. The method is not widely used because formaldehyde has such a high affinity for water that it will not go any further into the soil than the steam condensate that carries it, because of the time required to rid the soil of the vapor, and also the discomfort to the operators.

By clubbing together, growers can spread the high cost of equipment, as was done in Germany by Erven (1938) and as has since been done in the Buffalo, New York, area, where 12 men in 1950 bought a 25-horsepower flash boiler on wheels capable of treating 600 cubic feet of soil in five hours. Each grower pays a few cents a square foot, which amortizes the $3000 investment in six years and pays for fuel and a man to operate the machine. In England and Europe for many years a grower has been able to rent a 20-horsepower locomotive type boiler for soil-steaming purposes at certain times of the year. Very recently in the United States a low-priced, ten-horsepower, oil-burning boiler on two wheels has been gaining favor of many florists for steaming benches and potting soil (Ball, 1953).

Taking advantage of the slowness of cooling of hot soil, investigators have recommended shutting off the source of heat, be it steam or electricity, and utilizing the fireless cooker principle to finish off a batch of soil when once it is brought up to 160° or 180° F (Horsfall, 1935; Lawrence and Newell, 1938). Pasteurizing temperatures developing in compost piles is a gratuitous form of heat that often kills pathogens.

DANGERS OF REINOCULATION. Edgerton (1915) first pointed out that *Pythium* grows much faster in steamed than in unsteamed soil. Bewley (1923) found that *Verticillium* travels through freshly steamed soil three times as far in six weeks as in untreated soil. Hartley and Pierce (1917) decided that steaming outdoor forestry seedbeds is not recommendable because of the extent of loss from reinoculation with seedling pathogens. Walker and Smith (1930) and others have made use of this phenomenon by

regularly steaming soil previous to its inoculation with *Fusarium conglutinans* in testing cabbage seedlings for susceptibility in their program of breeding for resistance. Dimock (1941) found *Rhizoctonia* to grow as fast through unsteamed as steamed soil when host plants were close together. Hartley (1921) pointed out that the presence of saprophytic fungi, particularly *Rhizopus nigricans*, could be counted on to lower the parasitism of *Pythium debaryanum* when the latter was reinoculated into steamed soil.

If sources of atomic heat ever become cheap enough, steam could be employed more extensively outside of greenhouses. The techniques are known for applying it, but the cost of fuel limits its use to land producing high value crops.

HOT WATER

Byars and Gilbert (1920) eradicated *Heterodera, Rhizoctonia* and *Pythium* from soil in five-inch pots by five-minute immersion in water at 98° C, from eight-inch pots by pouring two to three liters of boiling water over each, and from shallow benches by application of seven gallons per cubic foot. Fleming (1925) showed that all stages of the Japanese beetle were killed in water at 112° F, a temperature not too injurious to plant roots. Compton (1936) devised a portable hot water sterilizer to be used at the end of a steam line for killing nematodes in soil. This is pictured by Ball (1939) and by Newhall, Chupp and Guterman (1940). Newhall (1930) compared steaming by the buried pipe method with a hot water drench in a ground bed of a sandy soil near Cleveland, Ohio, and found more than twice as many nematode galls on 1000 tomato plants from the hot water-treated as from the steamed soil. Its relative inefficiency (one pound of boiling water containing only one-sixth as many B.T.U.'s as a pound of steam at the same temperature), coupled with the more puddled condition of soil treated with hot water make its use unpopular. Bewley (1923) found that it took two million gallons of water per acre or four and one-half gallons per square foot by a surface drench method; and by mixing four to ten tons of caustic lime in the soil first and leading the hot water into parallel trenches, a deeper job could be done with 180,000 gallons of hot water per acre. But in a four-year test of the comparative values of steam and hot water on the yields of tomato, steaming was

found to be far superior. Modern methods of steaming soils are reviewed by Bronsart (1931) for Germany, by Bewley (1941) for England, for Norway by Roll-Hansen (1949).

ELECTRIC STERILIZERS

Stone and Smith (1898) tried to electrocute the root knot nematode in greenhouse soil and concluded that it could be done only by raising the entire mass of the soil to the thermal death point of the nematode, which is about 120° F.

Elveden (1921) compared electric with a number of other ingenious methods of treating soil but left no detailed account of his electrical equipment. The depression of the early 1930's induced electric power companies in America and Europe to encourage research on many agricultural uses of electricity, including soil pasteurization. Out of this, two general methods of electric pasteurization emerged. In the first, direct heating or soil resistance method, the current is passed through the soil between two or more electrodes. The soil becomes heated by reason of the resistance it offers to the passage of the current. In the second, the indirect heating method, covered resistance type heating units are buried in the soil and impart their heat to it by thermal conductance as the current is passed through them at a constant rate. Early work on the resistance method was done about 1931 in Holland by Kroft and Groen (1933) of a Holland power company, and in the United States by C. W. Wildebour of the Puget Sound Power and Light Company in cooperation with C. F. Doucette of the U. S. Department of Agriculture, Etomology Laboratory, at Sumner, Washington, according to Scott (1932). The American workers were able to raise 20 square feet of bench soil from 60° to 180° F in two hours with an expenditure of 70 kilowatt hours on 230-volt alternating current. This was repeated by Fee (1933), and by Krewatch and Kable (1933) who pointed out in a comprehensive report a number of difficulties and limitations involved in employing this method, such as the need for an extra heavy service line, the need for soil moisture, and proper compaction of the soil against the electrodes. In Germany, Dix and Rauterberg (1933) used a three-phase circuit and a transformer with variable capacity between 3.6 and 60 amperes at voltages between 2750 and 200. They varied the distance be-

tween their vertical parallel electrodes from eight to 78 inches. By using strong currents for relatively short periods of time, greater economy was obtained, and a cubic yard of soil was heated to 70° or 80° C with the expenditure of but nine to 16 kilowatt hours, or less than one-half kilowatt hour per cubic foot. The necessity of having a transformer and the hazards to the operator discouraged further work with exposed vertical electrodes.

Scott (1932) built the first cabinet type electric pasteurizer with vertical plates, many of which are still in use, but Blauser (1934, 1935) made an improvement by substituting two horizontal electrodes, on the top and bottom of the box, for the numerous vertical electrodes used by Scott. Blauser, and Tavernetti (1935) both pointed out that resistance to the current is directly proportional to the distance apart of these electrodes and at the same time is inversely proportional to their area. These facts, together with the limitations on maximum current available to most users, determines the proper size and depth of a cabinet of this type. Similar experiments were conducted in Holland with horizontal electrodes in a cabinet type pasteurizer by Kroft and Groen, and by Muyzenberg and Rijn (1937) who studied the effects of electrolytes, moisture and compression on conductivity of sandy soils. Their figures on current consumption were rather high, being 1.6 to four kilowatt hours per cubic foot, but their end temperatures were also high, being 99° C. They confirmed Blauser's conclusions that sand must be watered with a dilute electrolyte, such as potassium chloride or potassium nitrate, to insure rapid satisfactory conductance.

To eliminate the hazards inevitable where one is handling 230-volt, 30- to 60-ampere lines, Carney (1932) built a cabinet type pasteurizer with covered heating elements having a fixed current demand. This was tested by Horsfall (1935), and by Newhall and Nixon (1935) who made many comparisons between this and the direct heating type, concluding that the indirect type is better adapted to general use because of its greater safety and its known fixed demand on the current supply.

Ordinary soil-heating cable was found unable to withstand the temperatures required for soil pasteurization. The induction principle, so successfully employed in certain types of heating, was also found to be impractical because of the expense of equipment and the high current demand.

A continuous or semi-flash type electric soil pasteurizer, in which small piles of soil are dragged across an electrically heated steel plate at a rate which assures their reaching a temperature of 180° F by the time they fall into waiting flats at the end, was described by Newhall (1940), and another by Caple (1940), as rather successful. A similar continuous pasteurizer, described by Tavernetti (1942), heated one cubic foot of soil per thousand watts of heating capacity. He pointed out (1950) that if a cubic foot of dry soil requires 1800 B.T.U.'s to heat it from 50° to 200° F, it will require 1350 more B.T.U.'s if it contains 15 per cent moisture.

Experiments involving the generation of steam by electric heaters, either in a closed cabinet filled with flats of soil or under an inverted pan over soil in a ground bed, are of some interest because in neither case was the steam under any pressure, and yet rather good penetration of the soil was achieved to depths of ten inches at an expenditure of 1.76 kilowatt hours of current. This, in general, compares favorably with the cost of steaming with coal as fuel in small operations, although it is slower. With current costs of two cents per kilowatt, electric steaming of soil is economical of everything but the operator's time.

A number of attempts have been made to use very high frequency current, very high voltages between plow points, and other devices, but none of them has proved effective or practical. In some cases the designers have been more interested in making something that had sales appeal than they have in testing and establishing the validity of the principle involved.

The one factor limiting the use of electricity in soil sterilization is not the cost of the current but the size of the service line required to get an appreciable amount of pasteurizing done in a reasonable amount of time. It is like steaming an acre of soil with only a quarter-inch steam line. If one could operate on the offpeak load at the low rates for electricity after midnight and have the operation all automatic, so no hand labor was employed, it would be an economical way of pasteurizing piles of compost soil.

FLOODING

Plant pathogenic organisms require oxygen for respiration, hence are rather easily drowned. Some, however, like the water molds, thrive in the presence of water, and some nematodes and

higher fungi produce resting stages and sclerotia that can withstand a considerable period of submersion. Addition of numerous fungicides, insecticides or nematicides to the water is designed to hasten or otherwise improve the lethal action. Most of these substances go no farther into the soil than the water they are dissolved in. Some substances may be so promptly altered by the action of organic chemicals and soil organisms as to be rendered ineffectual in a few days or even hours under warm moist conditions.

According to Martin (1940), flooding was practiced by European grape growers with some success in their fight against the Phylloxera in the last century, and against wireworms recently in California by Campbell and Stone (1938). The work of Brown (1933) is of interest because he concluded that flooding for a long enough period to eliminate eggs of the root knot nematode from the organic soils of the delta region of the Sacramento and San Joaquin Valley in California would take the land out of production for nearly two years, which was not feasible. Michelbacher, Bacon and Underhill (1953), however, found that a seven- to ten-day period of flooding in the same region was adequate in the summer to eliminate the garden centipede which could be killed in as few as 48 hours at a temperature of 100° F. Moore (1949) was successful at eliminating *Sclerotinia sclerotiorum,* the cause of a severe stem rot of beans and other vegetables in certain Florida soils that have a compact subsoil. He found that these sclerotia would rot in 23 to 45 days in either muck soil or marl, regardless of whether flooding was continuous or at three-day intervals. Addition of green organic matter to the surface had no important effect on the process. Pink rot of celery was also controlled in Florida by Brooks (1942). The effects of flooding and of drying soils for the control of root knot nematode are well summarized by Kincaid (1946).

One of the largest most interesting flood-following projects in the world is that of the United Fruit Co. in Honduras for the eradication of *Fusarium oxysporum* f. *cubensis,* the fungus causing Panama disease, or banana wilt. If land, after flooding three to six months, remains relatively free of the disease for six years, it will pay to flood and replant thousands of abandoned acres in countries politically stable enough to warrant spending the millions of dollars required for such large-scale operations. Two of the conditions that must be remedied, according to Stover, Thornton

and Dunlap (1952, 1953), are that the rivers used to replenish the water, lost by evaporation and percolation, may contain as many as 150 spores per mililiter and that flooded soils are more favorable to growth of *Fusarium* after drainage than non-flooded (Stover, 1953). No soluble fungicide has yet been found to show much promise under the conditions of rapid decomposition obtaining in these tropical waters.

Oostenbrink and Besemer (1950) found that the cysts of the golden nematode (*Heterodera rostochiensis*) could withstand 15 months in water, so that flooding seems hopeless as a control for this pest. There is always the danger of spreading some unsuspected pathogen in a flooding program, which makes it somewhat hazardous. For example, Perry (1953) points out that the awl nematode (*Dolichodorus heterocephalus*), the cause of heavy losses in Florida, evidently prefers damp soils in wet locations. Hence flooding might actually increase its spread.

SOIL FUMIGATION

CARBON DISULFIDE

This fumigant is of considerable importance, not perhaps for its current usefulness so much as for its historical interest. Up to 1945 it was the most widely used of all soil fumigants, particularly against Scarabaeid larvae (Gough, 1945). It is surprising how many of the methods, rules and techniques so hopefully worked out the past 20 years for other soil fumigants were well developed or discarded half a century ago when the grape-growing industry of France and Germany was fighting Phylloxera for its life. As early as 1877 Dr. Crolas formulated ten rules for the use of carbon disulfide in soil fumigation, which rules have remained sound for 60 years. Good early histories of carbon disulfide soil fumigation are given by Bourcart (1913), Vermorel and Crolas (1915), Vogt (1924), Fleming and Baker (1935) and Gough (1945). From these we learn that by 1884 a million acres of soil were treated; in 1890 some 250 tons of " vaselinated sulfides ", containing 30 to 70% CS_2, were used in French vineyards, and in 1895 approximately 150,000 acres of vineyards were fumigated. The practice was then believed to be taking its place in agriculture like that of fertilizers. But four years later it was being discarded after the introduction of Phylloxera-resistant root stocks from America.

Although usually injected into holes 20 inches apart, the method

of spraying carbon disulfide in the furrow while plowing was enthusiastically adopted by many larger vineyardists until it was painfully learned that this method was inadequate. A less phytotoxic method of application, proposed in 1875 and developed rather extensively, employed irrigation water piped to the fields, sometimes several miles, containing a 0.5 per cent solution in the summer and a 0.7 per cent solution in the winter. A dosage of 2600 gallons per acre contained approximately 88 pounds of carbon disulfide.

It was learned that any gas dissolved in water does not penetrate soil any further than the water itself. Accordingly impregnated cubes of wood, heavy oils and even gelatin capsules were tried in place of water, but none was better than carbon disulfide alone, and no other chemical of the many tried was its equal. Many workers came to believe it had fungicidal properties against *Dematophthora necatrix, Fusarium dianthi* and *Rhizoctonia* species, as well as being lethal to the root knot nematode. By 1905, 99,000 lbs. were used in the province of Palatinate, Germany, where no specific parasites were known, according to Loew (1909).

It was recommended against beet root knot at 1580 pounds per acre, and wetting the soil after the injections were made was common practice. The many types of equipment employed, all illustrated by Vermorel and Crolas (1915), remind us of modern machines.

Over the 60-year period when carbon disulfide was much used, a great deal was learned of a rather fundamental nature about its effects on pests and on their hosts, about equipment for applying soil fumigants, and about the proper soil conditions for fumigation in general (Fleming, 1923, 1925). Its use increased crop growth as well as development of nitrifying bacteria and nitrates, while it reduced water retention in soils, inhibited denitrification, and suppressed most bacteria and protozoa. It thus greatly changed a soil's biological equilibrium and perhaps helped plants obtain more potash and phosphorus. As pointed out by Fleming (1925) and Fleming and Baker (1935), carbon disulfide has been used with success against ants, raspberry borer, white grubs, June beetle larvae, Oriental beetle, mealy bug, symphillids and cock chafer, while it has not been so successful in eradicating wireworms, cabbage maggot, peach borers, root aphids and sugar cane beetles because soil conditions and resistance make its action so

variable. Some plants, such as cyclamen, are injured instead of being stimulated. Soil temperature and moisture were found important in determining the efficacy of a given dosage against Japanese beetle larvae. Elevation of the temperature above 50° increased and elevation of soil moisture decreased the kill. A second treatment of a given soil persists five times as long as the first, the soil removing in some way much of the first charge, some of the second, but almost none of the third (Bywater and Pollard, 1937).

The movement of carbon disulfide vapor through soils was shown by Hagan (1941) and Hanneson et al. (1945) to be chiefly dependent upon the degree of porosity of the soil, which in turn is largely influenced by compaction and water content. A wet plow soil is impervious to the gas. Differences in partial pressures of the gas in different places, soil temperatures and degree of adsorption play minor roles. Soil permeability decreases to almost zero as soil moisture rises and approaches the moisture equivalent.

Use of carbon disulfide in emulsified form was popular at one time. While its efficiency is said to be cut in half by emulsification, its safety to plants is so much increased and the accuracy with which it may be applied so enhanced that it has been recommended in the United States in this form probably more often than by injection. This development was greatly spurred on by the appearance and rapid spread in New Jersey of the Japanese beetle and by the necessity of finding a safe and not too costly way of controlling it in nursery stock shipped out from that region and in lawns and golf courses. Johnson (1927) treated a total of 100 acres on 366 properties in Connecticut with an emulsion, using fire hydrants and a " Thomas proportioning machine " with a capacity of 600, and in one case 1200, gallons an hour. Fleming and Baker, and Merritt et al. (1933) treated similar large areas of lawn, the latter using two and one-half-inch porous hose rather than nozzles. While most insects succumbed to moderate dosages, the larvae of the Coleoptera (wireworms) required five to ten times more. Lathrop (1942) found that carbon disulfide emulsion actually increased the number of blueberry thrips. Schwardt and Lincoln (1940) found it the best of six fumigants in the control of the alfalfa snout beetle, but it took 1800 pounds per acre to kill 98 per cent of them. The buried tile lines in the ground beds of a greenhouse were used by Riley (1928) to introduce this fumigant

into the soil in the successful destruction of the garden centipede. Lines were 22 inches apart and 175 feet long, and by passing steam through the carbon disulfide container, 15 pounds of the gas were volatilized in a few minutes and driven into each line of tile one at a time. Thus an area of nearly 200 square feet was fumigated with 90 pounds or 1900 pounds per acre.

Some success attended the use of CS_2 emulsion in California against *Armillaria* root rot of citrus trees (Fawcett, 1936; Thomas and Lawyer, 1939) and against *Omphalia* root rot of date palms (Bliss, 1944*a, b,* 1947, 1948), it being judged the most satisfactory of three fumigants tried in the field. It penetrated much deeper than chloropicrin and was easier to measure than ethylene oxide. At rates of 1000 to 3000 pounds per acre, carbon disulfide will control nearly all of the root knot nematode in a greenhouse, but, according to Young (1939, 1940), these amounts are not able to kill all of the weed seeds or to control *Fusarium lycopersicum* on tomatoes, and it is hazardous to use. Accordingly, this material never became very popular with greenhouse vegetable growers who were fighting root knot nematode. The hazards were partly overcome, but not its poor fungicidal properties, by using emulsions (Schaffnit and Weber, 1929; Chapman and Parker, 1929; Gleisberg, 1930). Guba (1932) endeavored to correct this situation by combining carbon disulfide emulsion with formaldehyde, but the expense and labor involved deterred its general adoption. The fact that carbon disulfide is dangerously inflammable and explosive, especially if mixed with three times its volume of oxygen or an equivalent amount of air, having an ignition point of only 300° F and still lower on the surface of glass, copper, steel or chromium, makes its use rather hazardous. On the other hand, its volatility is in its favor. It has a vapor pressure of nearly 300 millimeters at 20° C, which means that 1000 cubic feet of air can hold up to 77 pounds of the vapor. Its fungicidal properties probably derive from its slight solubility in water, while its fumigating power against insects and nematodes may derive from its great solubility in fats, waxes and oils. All good soil fumigants seem to have this latter property in common. The actual lethal mechanism involved, once the chemical diffuses into a fungus or is taken into an insect by respiration, is largely a matter of conjecture, but there are probably several ways that death is brought about.

CHLOROPICRIN OR TEAR GAS

After World War I, large stocks of chloropicrin were on hand in several countries, the United States alone having reached a manufacturing capacity of three million pounds a month by 1919. The results of many investigators soon established its high unit toxicity to all sorts of living organisms, including insects, fungi, nematodes, bacteria and weed seeds. Some of this work may have been stimulated by the interesting observation than English factory workers, who filled artillery shells with chloropicrin, were singularly free from influenza, only two to four per cent of them contracting the disease as compared with 25 to 68 per cent among other workers (Shufflebothom, 1919). Among the 533 references to chloropicrin listed by Roark (1934) are 24 papers dealing with the toxic properties of this gas to microorganisms. Besides the bibliographies of Gersdorff (1930), Jackson (1934) and Roark and Bushey (1935), more than one hundred other papers dealing with this gas as a fumigant have been reprinted, whole or in part, since 1938 in the Larvacide Log published by Innis Speiden Company, now Larvacide Products Co.

Moore (1918) showed chloropicrin to be 283 times as toxic to certain insects, in air, as carbon disulfide. It promptly became a leading space fumigant for warehouses and flour mills, a place only recently disputed by methyl bromide (Johnson, 1937) and ethylene dibromide (Anon., 1946). Its extended use as a soil fumigant was brought on largely by a crisis in the Hawaiian pineapple industry (Nelson, 1951). Johnson (1935) found chloropicrin and carbon disulfide the best of 40 chemicals tested between 1927 and 1932 against the root knot nematode and other pineapple root troubles. Others were quick to show that chloropicrin was very effective in restoring yields of pineapples and of vegetables grown on " worn out " soils, and to emphasize its biotic rather than chemical role (Johnson and Godfrey, 1932; Cooke, 1933; Godfrey, 1934a, b, 1935, 1936; Howard, 1938; Stark, Smith and Howard, 1939; Stark, Howard and Smith, 1940; Smith and Howard, 1942).

Chloropicrin has been marketed chiefly in cylinders of various sizes, in one-pound dispenser bottles and as an aersol under pressure.

CONFINEMENT INCREASES EFFECTIVENESS AND ECONOMY. The high cost of chloropicrin together with its high vapor pressure and

hence rapid escape from the soil make some sort of seal imperative if dosage rates are to held to economic levels. Godfrey (1934) and Godfrey et al. (1934) found that the following made good coatings for paper to confine chloropicrin: cellulose acetate, 10 to 15 per cent solutions of animal glue, water glass, and various hydrophyllic colloids like starch paste, gelatin, and several other glues. Poor results were secured with varnish, paint, lacquer, enamel, rubber paint, graphite roofing paints, and shellac. Casein glue was about the only thing at that time found highly efficient by the United States Forest Products Laboratory in holding back carbon disulfide.

For several years glue-coated paper was used on seed beds, cold frames, bench soil, etc. when fumigated with chloropicrin. Merely sprinkling the surface of treated soil with from one to two pints of water per square foot within 15 minutes of fumigating has given fairly satisfactory retention of the gas, perhaps 85 per cent (Godfrey and Young, 1943; Stark, 1948; Lear, 1951). With the coming of plastics the picture changed, especially with the wider use of methyl bromide fumigants. First came the plastic-coated fabrics, as " Stericloth " and " Fiberthin ", then the straight plastic tarpaulins, exemplified by " Visqueen ", " Velan " and other cellulose and vinyl acetates. For weed seed control in seed beds, greenhouse benches or ground beds, the material is commonly injected in holes nine to 12 inches apart, four to six inches deep, at two to four milliliters per injection (Cooke, 1933; Garner, 1940; Godfrey, 1939; Godfrey and Young, 1943; Shippy, 1941; Clayton et al., 1949; Leukel, 1942; Jacks, 1953). Larger areas in or outside of greenhouses are treated with power-driven, multiple-row, sub-surface, continuous-flow injectors which have reached their highest state of development in Hawaii (Nelson, 1951). Closed gas-tight fumigation chambers for potting soil and mushroom-casing soil are sometimes used where fungi and insects are a problem and steam is not available (Thomas, 1942; Kligman, 1942).

The latest method of dispensing chloropicrin is from a cylinder as an aersol propelled by methyl chloride in the fumigation of potting soil, composts and seed beds under gas proof tarpaulins (Newhall, 1953).

The properties of chloropicrin which make it a good herbicide

render it extremely phytotoxic to living plants which must be removed from greenhouses prior to soil treatment. Moreover, the gas must escape completely from treated soil before the latter can be used. This may take from five to 20 days, depending on several factors—temperature, rainfall, tillage.

The killing range of chloropicrin for nematodes has been found by several workers to be about six inches from point of injection in ordinary soils, and to vary surprisingly little with increased dosages (Newton et al., 1937; Chitwood, 1939; Taylor, 1939; Stark, 1948). To kill the resting sclerotia of several important pathogens, e.g., *Rhizoctonia, Botrytis* and *Sclerotinia,* requires about twice the dosage needed for their vegetative stages. Even then the moisture content is important.

In his study of the dispersion of fumigants through a lateritic soil in Hawaii, Schmidt (1947) found that chloropicrin moved more rapidly through soil with 20 to 25 per cent moisture than through one with 10 to 12 per cent, as measured by kill of rice weevil. The reason assigned was that in a soil with so much colloidal matter, agglomeration of soil particles occurs at the higher moisture content which opens up larger pores. Smith (1938) found a soil temperature of about 20° C and soil moisture of ten to 15 per cent optimum for the death of soil bacteria and fungi. Of 600 soil fungicides tested by Schmitt (1949), only nine were very effective, and of these chloropicrin was lethal to the mycelium of five common pathogens in soil at one-eighth the dosage of its nearest competitor, allyl bromide. There seems to be general agreement that chloropicrin is more fungicidal and herbicidal than any of the other common soil fumigants (Shippy, 1941; Godfrey and Young, 1943; Tam, 1945; Newhall, 1946; Stark and Lear, 1947; Jacks, 1945, 1948*b, c;* Lindgren and Henry, 1949; Jacks and Smith, 1952; Jacks, 1952). Out of 30 kinds of seeds tested by Welton and Carroll (1941), only those of lamb's-quarters, orache and white clover were resistant to a dose of 25 to 30 ounces of chloropicrin per cubic yard. Morrison and Mote (1941) found chloropicrin toxic to symphylids in soil but concluded that it requires a rate of 300 pounds per acre at a cost of $200 to $300 to control them. He found chloropicrin dispersed to greater distances than D-D, but Stark and Lear (1947) found D-D to penetrate much deeper than chloropicrin in a closed container.

Stark (1948) reported adsorption to play a very important role in the practical application of chloropicrin because, whereas the dry sand fraction of a certain mineral soil could absorb but 0.18 per cent of its weight of chloropicrin, the silt fraction but 0.8 per cent and the clay fraction only 3.2 per cent, the colloidal clay fraction might adsorb nearly ten per cent of its dry weight at 30° C. So it takes up to 50 per cent more chloropicrin to achieve good results in some clay soils. The process was exothermic, reversible, unimolecular and almost linear in relation to temperature, though at lower temperatures more adsorption might take place as a result of capillary condensation.

Crops growing in closely planted rows, such as carrots, sugar beets and tobacco, need over-all soil treatments, but Taylor (1941), Taylor and McBeth (1941) and Walter and Kelsheimer (1949) have shown how costs of treatment for tree sites, vine crops and hill crops, such as watermelons, can be reduced by 50 to 80 per cent by spot injections. In such cases a water seal becomes more feasible and greatly adds to the efficiency. Since even an over-all treatment for nematodes never eradicates completely and has to be repeated, it is clear that the economy of spot treatments in the course of time can be very great. For crops like pineapples and tomatoes, even an in-the-row treatment can bring about considerable economy over an over-all treatment. However, inferior increases in yields of fall grown cucumbers were reported from row treatments with D-D by Epps (1950).

The effect of fumigation with chloropicrin on the soil flora, on biologic activity and on chemical constituents has been rather thoroughly studied by Johnson (1935), Cooke (1933), Smith (1938), Matthews (1924), Stark, Howard and Smith (1939), Schchepetik'nikova (1942), Schchepetik'nikova and Scheremisova (1937), Stark and Smith (1938), and Tam and Clark (1943). The earlier work showed that, as in steaming, there may be temporary inhibition of nitrification after treatment, an increase in ammonia and a very large increase in root growth, since total nitrogen is sometimes raised. Plants were found to pick up one and one-half to three times as much nitrogen and one and one-half times more P_2O_5, from which Russian workers argue that chloropicrin helps to mobilize more nutrients by intensifying microbial activity and organic decomposition. A large portion

of the soil's nutrients must be locked up in the bodies of micro-organisms, much of which is liberated on their death.

Use of emulsions to hasten penetration and give direction to applications has been tried (Jacks, 1951). Todd, Lucas and Moore (1950) obtained control of tobacco black shank, but not of weeds, with 38 milliliters per gallon per square yard of tobacco seed bed. The fact that it may take three to four times as much per acre has mitigated against wide acceptance of this method of application (Taylor, 1941).

Sugar beet-receiving stations in some places have had a problem of disposing of their screenings when they contained sclerotia of the fungus *Sclerotium rolfsii*. Davey and Leach (1941) found chloropicrin effective at disinfesting the piles but not recommend-able because of the difficulty of confining the gas, a problem that would seem to have been met, now that plastic tarpaulins of almost any length and width are available, and since chloropicrin may be obtained in pressurized containers.

RESPONSES OF FIELD CROPS TO CHLOROPICRIN. Although not recommended for field crops on account of the expense, Mc-Laughlin and Melhus (1943) pointed out that fall applications of chloropicrin at three milliliters per injection on ten-inch centers caused better germination and growth of spring-sown oats, barley, wheat, rye, flax, cowpea, alfalfa and sugar beet. Barley yields were increased 450 per cent and sugar beets 606 per cent. Isolations showed that there was less *Pythium* and other seedling-rot genera in treated plots. On the other hand, with spring treatments Bruehl (1952) obtained reductions in yields only of wheat and barley.

VIRUSES DESTROYED. Several fumigants, including chloropicrin, were found by Johnson (1945) to control wheat mosaic, pre-sumably by destroying some unknown vector. Allen (1948) found chloropicrin and other fumigants, such as D-D, but not ethylene dibromide, capable of destroying the soil virus causing big vein of lettuce. Rich (1950) noted that chloropicrin in xylol, 1 : 4, would do the same at 500 lbs. per acre, but not chloropicrin alone.

ECONOMICS. Efforts to reduce the cost of fumigation with chloropicrin have included adding cheaper diluents with nemacidal

powers of their own, such as ethylene dichloride (Chitwood, 1941; Newhall and Stark, 1942), and adding D-D mixture. The possibility of getting synergistic effects has not been explored very thoroughly, since much cheaper replacements for chloropicrin have been appearing, e.g., methyl bromide, D-D mixture and ethylene dibromide.

There have been several cases where soil fumigation with chloropicrin was disappointing, too costly or devastating, due to recontamination with certain pathogens, the latter being particularly true with cereal crops (Bruehl, 1952). Pea root rots were not well controlled (Reinking and Newhall, 1950), nor sclerotia in surface piles of beet screenings (Davey and Leach, 1941), nor the potato wart (*Synchytrium*) (Gimingham and Spinks, 1919). Expense rules it out against beet nematode and wireworm (Karab and Butovski, 1940; Kapshuk, 1933; Decoux and Roland, 1938; Stone and Campbell, 1933; Morrison and Mote, 1941). Since it acts as an irritant against insects, symphylids are driven to migrate further down in the soil and thus to escape. The fact that chloropicrin is 40% more soluble in cold water (0° C) than in warm (25° C) helps explain subsequent damage to plants if soil is treated when cold and later warms up after being planted (Shepard, 1951).

Because of its ability to destroy a great variety of soil pests, chloropicrin still is widely employed where the value of the crop is high and its use therefore justifiable. Its cost, inevitably high by reason of its nitrogen content and the expense of its manufacture, together with its lachrymatory, phytocidal and corrosive properties, have led to the discovery of safer, cheaper soil fumigants. But for 20 years it has been a yardstick by which the newer materials have been measured.

DICHLOROPROPENE-PROPANE MIXTURE

With the discovery of the nematocidal properties of D-D mixture by Carter (1943, 1945) in Hawaii, the practice of soil fumigation was greatly stimulated (Anon., 1946). This by-product in the manufacture of allyl alcohol, as one step in the petroleum plastic industry, is a 2:1 mixture of a 1,3-dichloropropene and 1,2-dichloropropane with minor amounts of lighter and heavier saturated and unsaturated hydro-carbons. The fraction toxic to nematodes, wireworms and fungi is the 1,3-dichloropropene (Lange, 1946;

Newhall and Lear, 1948; Zentmyer and Klotz, 1949; Lear, 1951). Boiling points, however, are close, and separation of the fractions is not practicable or necessary; there may even be some beneficial action from the other components (Carter, 1945). It has a boiling range of 95° to 150° C, and its volatility consequently is low enough to make sealing it in the soil unnecessary, thus giving it a great advantage over chloropicrin in addition to its lower cost. It is somewhat less disagreeable than chloropicrin to handle, but it can burn the skin and cause some discomfort from inhaling.

In general, D-D lacks fungicidal properties, according to Parris (1945) and Newhall and Lear (1948), but Clayton et al. (1949) found that it controlled *Sclerotium rolfsii* in one field on tobacco, though not *Rhizoctonia*. Stark and Lear (1947) obtained some control of *Fusarium* pea seedling rot with it in greenhouse tests, while Zentmyer and Klotz (1949) found that both D-D and Dowfume-N killed *Phytophthora cinnamomi* and *Phytophthora citrophthora* at dosage rates that did not eradicate the normal soil flora. Jacks (1945) got some damping-off control with it. From extensive work on lima bean root rot control in California, Middleton, Stone and Kendrick (1949) conclude that D-D has some fungicidal properties, as it was the only thing that controlled both wireworms and the fungi implicated in the root rot complex, being more effective than ethylene dibromide, although the latter is better against wireworms. Some success was likewise obtained against *Sclerotium rolfsii* attacking sweet potatoes by both D-D and ethylene dibromide in Louisiana, according to Martin (1953).

The nematocidal and insecticidal properties of D-D mixture are excellent in field use at dosage rates of from 200 to 600 pounds per acre; its cost is from $35 to $90. Its effectiveness and low cost against root knot nematode of tomato in greenhouses were demonstrated in comparison with other fumigants by Stark, Lear and Newhall (1944). Its use has greatly increased sugar beet yields where beet nematode (*Heterodera schachtii*) is serious (Anon., 1947; Thorne, 1952). Benefits from root knot control on tobacco are reported in Florida by Kincaid (1948), in North Carolina by Garris (1953), and on cucumbers by Epps (1950) in South Carolina. The meadow nematode was controlled on tobacco in Canada by Koch and Stover (1950) and by Clayton and Ellis (1947) who got good root knot control with 200 to 400 pounds

applied seven to ten months before sowing vegetable crops.   July and October treatments were better than March treatments. Warren (1950) found D-D better than ethylene dibromide against root knot on sweet potatoes and melons in Indiana.   Mullin (1953) controlled cracking of sweet potatoes, which was regarded as caused by some nematode not specified.   In California, Stone (1944) showed it to be superior to carbon disulfide for wireworms, and Lange (1945, 1947) reported that 25,000 acres were fumigated for wireworms and nematodes with either D-D or ethylene dibromide before planting the bean crop.   D-D is said to have given outstanding results in the Salinas Valley on fall lettuce when used at 400 pounds per acre, particularly when 35 pounds of anhydrous ammonia were applied with it to counteract the depressing effect on growth.   Cook (1949) found D-D more efficient than ethylene dibromide or dichloronitroethane in compact soil.   The penetrating power of D-D makes it more suitable for heavy soils than other fumigants and may explain why a 25-gallon rate per acre has worked better on sugar beet nematode-infested soil in Utah and Idaho, where soil types are heavier, than in California (Allen and Raski, 1950).

The question of residual effect or harmful accumulation from repeated annual applications is currently receiving attention. McBeth (1951) found no evidence of residue toxic to tomato, tobacco, melon or cowpea from five annual applications of 400 pounds of D-D per acre.   A similar report by Ellis et al. (1949) indicates no cumulative toxicity from three annual applications of D-D, ethylene dibromide, chloropicrin or ethylene chlorobromide.

Some failures have been reported from the use of D-D for nematodes, but most of these are in connection with cyst-forming species, such as *Heterodera rostochiensis*.   Peters and Fenwick (1949) reported only a 50 per cent reduction by applications as high as 800 pounds in certain English soils.   The kill was improved by covering with sisalkraft paper and once by rolling.   In the Isle of Jersey applications of 450 pounds per acre failed to reduce eelworm population, although yields of potatoes were increased somewhat, according to Small et al. (1950).   On Long Island, Mai (1950) reported that two annual fall applications of 250 pounds of D-D reduced the population of viable cysts from 19 per ounce to 0.04 per ounce of soil.   This, however, was not complete eradication

and so was unacceptable.   Under some conditions considerable
weed control has been obtained at dosage rates employed for nema-
todes and wireworms, but this can not always be counted on.   It
seems to be dependent upon the moisture content of the seeds.   If
they are about to germinate, kill is better than when they are rela-
tively dry and dormant (Carter, 1945; Newhall and Lear, 1948).

ETHYLENE DIBROMIDE

Like D-D mixture and closely following its introduction, ethylene
dibromide has had a meteoric rise as a very popular and useful
soil fumigant, chiefly against wireworms and nematodes (Anon.,
1946b).   It might have come into use sooner had it not all been
consumed during World War II in the making of tetra-lead-ethyl
anti-knock adjuvant for aviation and other gasolines.   First found
by Lange (1946, 1947) and Cook (1949) to be very effective in
California and Washington against wireworms, ethylene dibromide
was soon shown by Christie (1947), Newhall and Lear (1948b)
and many others to be a very potent nematocide (Townsend, 1948;
Leding, 1950; Strand, 1951; Miller, 1951; Curzon, 1951; Lem-
bright, 1953; Henry, 1953).   After 60 experiments involving 50
fumigants, Lear (1951) concluded that, on a volume basis, ethylene
dibromide was the most powerful nematocide of all, though closely
followed by D-D and methyl bromide solutions.   Many reports
from the use of this fumigant on tobacco, carrots, celery, cotton,
beans, beets, sweet potatoes and tomatoes have been summarized
by Biron (1951).   In California, only a few years ago, many
thousands of acres were fumigated for wireworms.   Recent use
of Chlordane, Heptochlor and Aldrin, however, constitute much
cheaper methods of control that have largely replaced D-D and
EDB (Lange, 1947; Wellman, 1948).

Ethylene dibromide, like D-D, has a high boiling point.   It
needs no sealing in and so is adapted to extensive field applications.
It has been marketed as a solution of various concentrations in a
naphtha thinner at strengths varying from 10 to 85 per cent active
ingredient (Anon., 1949).   When the more concentrated solutions,
85 per cent, are employed, only four to six and one-half gallons
an acre are needed.   Side dressings of sugar beets in California,
and pineapples in Hawaii with two, three and four gallons per acre
have increased the tonnage and sucrose content.   Use of ethylene

dibromide has become standard practice with many tobacco growers in Florida and Georgia, and on shade tobacco in Connecticut.

Ethylene dibromide is acknowledged by nearly all who have tested it as being very low in fungicidal activity (Schmitt, 1949; Jacks and Smith, 1952; Zentmyer and Klotz, 1949; Zentmyer and Kendrick, 1949; Wensley, 1953). However, a surprising and valuable discovery, reported by several workers the past few years, is the remarkable control of fungous diseases or root disease complexes obtained with this fumigant. Thus Smith (1948) and Presley (1950) obtained control of cotton wilt, induced by *Fusarium vasinfectum;* Meuli and Swezey (1949) of sweet potato black rot, caused by *Ceratostomella fimbriata.* A southern pine seedling root rot complex was controlled by Henry (1950, 1953). Koch and Stover (1950) and Jenkins (1948) controlled a brown root rot of tobacco, and Middleton et al. (1949) reduced losses from root rots on beans. Nusbaum and Chapin (1952) reduced black shank of tobacco, and Townsend (1948) controlled root rot in celery seed beds. It is believed by many of these workers that the benefits of fumigation with ethylene dibromide are indirect, being due to death of the nematodes or wireworms that are thought to be responsible for opening the way for certain parasitic fungi, some of which may be too weak to initiate infection by themselves. This and other observations by Christie (1953), Steiner (1945, 1949, 1953), Oostenbrink and Besemer (1953) and others to the effect that many soil-inhabiting nematodes are constantly doing more harm than hitherto believed possible, particularly the root lesion, sting, stubby root and meadow nematodes, which are widely distributed and harmful to a large variety of crops, all emphasize the importance and value of soil fumigation to agriculture in general. These observations should encourage its use, at least on a trial basis, in all sorts of disease situations where poor growth, slow decline or an unhealthy condition of obscure etiology exists. They scarcely warrant the wholesale propagation, however, of the doctrine that all fields of everything should be fumigated annually as a general sanitary measure. Treatment for wireworms with a three-year life cycle should not be required as often as for root knot nematode with a four- to six-weeks cycle.

The tobacco crop of the United States grown on the same soil for many years in a warm climate, and therefore subject to the ills

that nearly always follow a continuous cropping system, is probably gaining most from soil fumigation. All tobacco farms in North Carolina are said to be infested with nematodes, and the loss in 1952 was $25 million, according to Garris (1953). Here is where most of the D-D and ethylene dibromide are being used, nearly 100 thousand acres being fumigated in this one State in 1953. The question of which fumigant adversely affects the burning qualities of the cured leaf on account of its higher chloride content is a hot one (Anderson and Swanback, 1950; Kincaid, 1948). The delay in nitrification (Tam, 1945) brought on by the soil treatment is thought by Kincaid (1947) to be beneficial to shade tobacco.

Incorporation of ethylene dibromide in capsules was described by Lear (1951). The idea was so intriguing that one company bought a million of them before it was found that in field practice they do not all dissolve at the same time, which may result in crop injury later on, a phenomenon encountered 60 years earlier in the use of carbon disulfide against Phylloxera.

METHYL BROMIDE

The use of methyl bromide as a space fumigant in vaults and greenhouses preceded its use as a soil fumigant. In summarizing such work, Richardson and Johnson (1935) pointed out that it penetrates soil in a matter of hours, to kill insects and nematodes. Experiments soon followed to determine the proper dosage rates against a variety of pests, the extent of its phytotoxicity, and the best means of handling this odorless, colorless gas with its very low boiling point (4.6° C). At ordinary temperatures it must be dispensed as a vapor from sealed containers, such as steel cylinders or one-pound cans, or else it must be first dissolved, up to 15 per cent, in a cheap solvent such as propylene dichloride, carbon tetrachloride or xylene. The resulting solution can then be poured or injected into the soil. With the coming of gas-proof plastic tarpaulins of 100-foot lengths and up to 16-foot widths, seed beds, hot beds and bench soils can now be gassed under cover for periods of 24 to 48 hours at dosages of one to three pounds to the hundred square feet (Taylor and McBeth, 1940; Hamilton, 1940; English, 1944); Taylor and McBeth, 1941; Taylor, 1941; Gingrich and Haenseler, 1941; Godfrey and Young, 1943; Stark, Lear and

Newhall, 1944; Start and Lear, 1947; Koch, 1951; Magie, 1952; Marvel, 1953; Munnecke and Ferguson, 1953).

For ground beds and for small amounts of soil in covered garbage cans or steel drums, injections of small quantities of the liquid solution (" Bromex ", " MBX ") have found favor with florists. The dosage required for nematodes is phenomenally small, but to kill fungi requires one and one-half to two and one-half ml. of the pure methyl bromide, or its equivalent in solution, per cubic foot of soil, or about the same dosage rate as for chloropicrin (Newhall and Lear, 1948*a*, *b*; Leonard and Harris, 1950; Anderson and Swanback, 1951; Gruenhagen, 1953).

Several thousand acres of seed beds devoted to tobacco in the United States are now fumigated with methyl bromide, according to Koch (1951) and to Freeman (1948). Of 12 chemicals compared, Hill et al. (1951) found methyl bromide the best weed killer for tobacco beds, the others being more or less selective. The cost of fumigation with methyl bromide is not quite so high as with chloropicrin but still is too high to give it a place on land growing low value crops. The necessity of sealing it in with gas-proof tarpaulin, asphalt coated paper or a sprinkling of water adds to its inconvenience in large areas out-of-doors. However, Kopitke (1951) reports seven acres of tree nursery profitably fumigated under tarpaulins over a three-year period at $325 an acre per year with an annual saving of $550 of weeding cost; besides much better stands, faster growth and sturdier seedlings resulted. Legume seeds are the hardest to kill. In general, as a nursery seed-bed treatment, fumigation with methyl bromide has become exceedingly popular (Dieter and Coulter, 1949; Leonard and Harris, 1950; Hill, Klingman and Woltz, 1951; Stover and Koch, 1952; Swank and Perry, 1953).*

The advantages possessed by methyl bromide over other soil fumigants are its fast penetrating ability, making it unnecessary to wait for root knot nematode galls to rot in the soil; the speed with which it leaves the soil; and its low phytotoxicity, making it possible to treat soil in close proximity to growing plants and at lower temperatures than with other fumigants (Stark et al., 1944; Stark and Lear, 1947; Lear, 1951). Some greenhouse growers, recognizing the better fungicidal properties of chloropicrin, use it in the summer when soil temperatures are highest, and methyl

bromide in the winter when soil temperatures are low and time is short.

Daily fumigation of 300 to 500 flats of soil under a plastic tarpaulin is said to be common practice in certain California nurseries where four pounds to 100 cubic feet of space is used and the gas is passed through a copper tube immersed in water at 160° F to insure rapid volatization. Several of the worst sclerotia-forming soil fungi are controlled in this way, according to Munnecke and Ferguson (1953).

The problem of exterminating poultry parasites from the soil in poultry ranges is receiving some attention, according to Clapham (1950) who was successful in killing ova, in soil, of *Ascaridia lineata, Heterakis gallinae* and *Syngamus trachea*, in both freshly passed and embryonated states.

Cut ants were successfully eradicated in Texas by the liberation of a pound of methyl bromide in each of the burrows, according to Kennerly (1953).

Addition of alcohol to methyl bromide reduced its efficacy against the root knot nematode very much, according to Gingrich and Haenseler (1941).

Adsorption of methyl bromide, like that of chloropicrin, may take place on certain soils. The chief factors determining this are soil type and moisture content. Dry peat adsorbed 41 per cent of a given charge but wet peat only 20 per cent, according to Chisholm and Koblitsky (1943) who likewise found that wet and dry clay adsorbed 25 and 11 per cent, respectively, while sand adsorbed less than ten per cent, wet or dry. On the other hand, Fuhr, Bransford and Silver (1948) found a sandy clay soil with 11 per cent moisture to adsorb little or no methyl bromide, even though the same soil adsorbed hydrogen sulfide, hydrogen cyanide and sulfur dioxide to a marked extent. Relatively poor control of root knot nematode was obtained with a given dosage by Lear (1951) in a muck soil as compared to that in a sandy or clay soil. Others had reported poorer kill of bacteria and fungi in organic soils, the moisture content being of less mportance than the organic content (Dieter and Coulter, 1949; Wensley, 1953).

There are a few cases on record of apparent injury to certain plants grown in methyl bromide-fumigated soil. This was thought by Williamson (1953) to be due to adsorption of bromine by the

organic or the colloidal clay fractions of certain heavy soils. Plants particularly sensitive to bromine were chrysanthemum, carnation, viola and salvia. The retarding effect sometimes lasted several weeks. One variety of chrysanthemum out of 11 exposed to the fumes above ground was found exceedingly susceptible by Newhall (1951, 1952), indicating a striking varietal difference in subsceptibility.

Regardless of isolated cases of injury from fumigation with methyl bromide, the ease with which it can be handled and its efficiency against a wide variety of pests assure it an important place in the pharmacopoeia of agricultural chemicals.

An attempt to kill the root rot fungus, *Phytophthora cinnamomi,* under living avocado trees by fumigating with methyl bromide or chloropicrin, or by treatment with Vancide 51 or Dithane D 14 resulted in too much tree injury for treatments to be recommendable, according to Gustafson (1954).

FORMALDEHYDE

For many years formaldehyde has been used as a seed, soil and space disinfectant. Its precarious claim to a place among soil fumigants emanates from its use by Sayre and Thomas as a dust for controlling smut of cereals. Others have employed it for soil treatment as a six per cent dust adsorbed on some inert carrier such as charcoal, infusorial earth, ground oat hulls, sawdust or even dry muck soil. Rates of application per bushel of soil varied from six to 16 ounces of a dust containing about 15 per cent formalin, dry weight basis (Wilson, 1930, 1932; Wilson and Tilford, 1933; Alexander et al., 1931; Tilford, 1931, 1932; Brown, 1941). The mixing process with the soil was rather disagreeable, and proprietary preparations tended to deteriorate so that the use of formaldehyde dusts for soil disinfestation enjoyed but short popularity. Some workers found the results with it somewhat inconsistent (Person, 1939; Person and Chilton, 1942).

An essentially similar method of dispensing formaldehyde in fairly concentrated form for damping-off control was developed by Guterman and Massey (1935). They employed a very small amount of water in place of the dust as a carrier and emphasized thorough mixing with the soil. Both methods reduced the time interval between treatment and planting from ten days in the old drench method to 24 or 48 hours. For controlling damping-off in

seedbeds it was found that sprinkling the beds with a dilute formaldehyde solution, 1–200 to 1–600, immediately after sowing the seed was very effective in improving the emergence of many different seeds (Haenseler, 1935; Ogilvie et al., 1938; Anderson and Swanback, 1951).

Eradication of root-rotting organisms and nematodes deep in the soil has been attempted in connection with the root rot of cotton and of date palm in California (McKinnon and Lillelund, 1931; Kellerman, 1932; King and Hope, 1932). The latter employed a gallon per cubic foot of a one and one-fourth per cent solution under pressure with special apparatus which forced the solution into the soil as far as six feet. With injections a foot part, five acres required almost one and one-third million gallons of solution (Skillman, 1949).

Addition of formaldehyde to steam and to carbon disulfide emulsions to increase the speed of action and range of lethal effect has already been mentioned (Winston, 1913; Guba, 1932; Beachley, 1937; Hunt et al., 1925; Manns, 1947). The cost and bother of applying formaldehyde, either as a drench or by one of the methods requiring mechanical mixing with the soil, and the fact that it is not a very good nematocide have all militated against its extensive use, even in greenhouses. Attempts to reduce the cost somewhat were made in 1928 and 1932 by Doran who substituted acetic or pyroligneous acids for the formaldehyde, and by Bewley in 1935 who substituted crecylic or crude carbolic acid, but none of these is cheap enough or effective enough to win favor with practical growers. Jacks (1948) compared formaldehyde in an 0.8 per cent solution with paraform against Verticillium wilt of tomato and concluded that paraform was milder in both fungicidal and phytotoxic effects. Formaldehyde persisted longer. One of the most successful applications of formaldehyde against a fungous disease is its use in the control of onion smut. A very dilute solution, 1–128, when dribbled into the row, at the time of sowing the seed, at the rate of about 110 gallons to six or seven miles of row, gives almost perfect control of this disease (Walker, 1920; Anderson, 1923; Nelson, 1948).

MISCELLANEOUS FUMIGANTS

To name all the fumigants that have not quite come up to requirements for successful adoption is unnecessary, but some may

deserve mention as not having yet been thoroughly enough tried to fall in the hopeless group. Thus the tetra and penta chloro-ethanes were found by Godfrey and Young (1943) and by Stark and Lear (1947) to be potent nematocides. Also dichlorisopropyl ether was very effective. But these persist too long in the soil and are too phytocidal to seem very promising.

Allyl alcohol and allyl bromide have been shown to have fungi-cidal properties that can not be lightly dismissed, the latter being one of the best of 14 tested by Christie (1945, 1947) against root-knot nematode and several soil fungi. Allyl bromide was found to compare favorably with chloropicrin against Verticillium wilt of tomato, although it failed to diffuse upward as well, according to Schmitt (1949) and Wilhelm and Ferguson (1953).

A mixture of chlorinated and brominated hydrocarbons con-taining over 55 per cent chlorobromopropene has recently shown marked soil-fumigating properties against a variety of soil fungi as well as nematodes (Kreutzer and Montagne, 1950; Haasis, 1952). It needs no seal but is a disagreeable, rather phytotoxic lachrymator, the cost of which may limit its use, like chloropicrin. It was sprayed in the row at the time of sowing to control pea and bean Fusarium root rot by Watson (1951).

Since the preliminary testing of dichlorobromopropene by Christie, who found it rather effective against nematodes, Lear (1950) found it as good as D-D mixture against the golden nematode of potato, although it persisted longer in the soil.

Dibromobutene, another lachrymator with low vapor pressure, has been used in solid form as a dust incorporated with the soil for celery seedbeds and greenhouses where it has shown promise against a variety of soil fungi, according to Kreutzer et al. (1951) and to Swank (1951). Though volatile, it needs no seal. It was one of the four better fumigants compared in the field against the golden nematode when used in two split applications at 225 pounds each (Lear, 1950; Lear et al., 1952). But being more phytotoxic, disagreeable and expensive than D-D, its future seems somewhat doubtful at present.

Parathion is not ordinarily used as a fumigant and may not have acted in this way in an experiment by Dimock and Lear (1950), in which root-knot nematode was controlled by one gram of 15 per cent wettable powder mixed with a gallon of soil in which

susceptible plants were subsequently grown. The plants may have absorbed the chemical and become immune. This rate is over 30 times the normal one per acre. A dose 50 per cent larger killed *Heterodera rostochiensis,* the golden nematode of potato, while chlordane and benzene hexachloride failed even at larger dosages. Clayton and Ellis (1947) found benzene hexachloride unable to control root-knot, even at 675 pounds per acre where it became very phytotoxic.

Among the more interesting fumigants tested against the cysts of the potato golden nematode are the ammonium and calcium chloroacetates and the isothiocyanates, one of which, allyl isothiocyanate, is mustard oil, reported on by Smedley (1938, 1939) and Ellenby (1945, 1947). While these chemicals brought about yield increases, they never reduced the nematode population sufficiently to be recommendable. In fact, nothing has thus far appeared recommendable as an eradicant against this nematode, according to Chitwood and Buhrer (1945) who summarize five years work with fumigants on Long Island by saying that, although in some instances over 90 per cent control was obtained with D-D mixture, carbon disulfide, chloropicrin or methyl bromide, nevertheless, yield increases of potatoes covered the cost of treatment in only three out of five cases where D-D was used, three out of seven where carbon disulfide was used, four out of 25 where methyl bromide, and none out of seven where chloropicrin was used.

When 600 soil fumigants were tested against six common soil pathogenic fungi by Schmitt (1949), the following were lethal: allyl bromide at 61 gallons per acre; allyl and ethyl isothiocyanate at 76; formalin, Iscobrome and D-D at 380; allyl chloride and methyl bromoacetate at 456 gallons. Chloropicrin was the most effective, killing all fungi at 8.6 gallons.

DEVELOPMENT OF FUMIGANT DISPENSERS

The development of adequate machinery for accurately dispensing soil fumigants soon followed the discovery of the remarkable virtues of chloropicrin. Here the European experience with carbon disulfide dispensers, at the close of the last century, was very helpful (Vermorel and Crolas, 1915). The French " Pal "

by Vermorel was imitated and improved by several manufacturers who brought out the " Carbona prod ", the " Calispray ", the Innis Speiden 4 models of " Larvajector ", the Mack " Anti-Weed Gun " fumigator injector, and the McLean fumigator hand injector (Godfrey and Young, 1938; Jacks and Wright, 1947). Multiple-row, continuous-flow, sub-surface injectors and gravity flow as well as forced feed sprayers for plow applicators have been developed by the dozen and are described or illustrated by Johnson (1935), Neller and Allison (1935), Godfrey and Young (1943), Carter (1945), Newhall (1946), Cook and Lane (1947), Walter and Kelsheimer (1949), Clark and Myers (1951), Watson (1951) and Jacks (1952). Some of the more recent models are pictured anonymously in Down to Earth (1947) and Farm Management (1953). Jenson (1953) found that power-drawn equipment failed to duplicate results obtained with hand gun. Piston type pumps actuated by a cam on a spiked auxiliary wheel off to the side of the plow (Hasson, 1920; Starnes et al., 1951; Jacks, 1952) have given way nearly everywhere to inexpensive gear pumps that maintain a steady pressure of 20–30 lbs. on one to ten lines of fumigant. The fumigant is sprayed on to the plow sole or is forced through copper tubes behind a series of spear shanks drawn through the soil by a tractor at a constant speed (Newhall and Lear, 1948; Lear, Mai, Feldmesser and Spruyt, 1952). In one inexpensive outfit for cotton the fumigating, fertilizing and bedding or " boarding off " are all done in one operation (Kelsheimer and Walter, 1949), and in Hawaii a number of operations, as land fitting, fertilizing, fumigating and mulch paper-laying, are done at one time (Nelson, 1951).

It is the careful refinement of this fumigation equipment that has permitted accurate employment of more and more concentrated fumigants at reduced amounts per acre. As little as six or even three gallons of an 85% ethylene dibromide solution are sometimes used (Kay, 1951; Lembright, 1953). At such rates there is a saving of weight, of labor, of shipping charges and of storage space (Biron, 1951). Compact fumigation kits are now available to farmers, ready to be attached to their tractors. The remarkable development of such equipment has had much to do with the fact that 200 to 300 thousand acres of farm land were probably fumigated in the United States in 1953.

CHEMICAL AND BIOLOGICAL CHANGES INDUCED
BY SOIL DISINFESTATION

The main purpose of soil disinfestation has always been to kill detrimental microflora and to control weed seeds, although it has not always been expressed as bluntly as this. In the search for an explanation of the remarkable increases in plant growth following soil treatments with heat or fumigants, chemists, bacteriologists, agronomists, plant physiologists and biologists have propounded a number of ingenious theories. These have been well reviewed by Schreiner, Oswald and Lathrop (1912), by DuBuisson (1917) and by Kopeloff and Coleman (1917). These theories need no further elaboration. Many of the older investigators have expressed a touching concern for the useful microorganisms that must inevitably suffer the same fate as their parasitic relatives in any effective soil treatment. Some workers seemed bent on explaining crop responses to soil treatments the hardest way possible. However, we are indebted to them for a number of well established facts.

Treating soils, either by heat or by " antiseptics ", has the following results:

(a) Non-spore-forming, nitrogen-fixing, nitrite-forming and nitrate-forming bacteria, as well as parasitic organisms are destroyed, and nitrification is thereby inhibited. The spore-forming ammonifiers which escape, therefore, have a field day, and ammonification goes on almost uninterrupted for weeks, especially in soils high in organic matter.

(b) Soluble salts are often liberated by heat in quantities two to ten times their previous level, being in some cases chlorides and sulfates of ammonia and sometimes soluble manganese (Gregory, 1936; Hoffman, 1939).

(c) Treated soils often have a reduced capillarity and water-holding capacity resulting from destruction of some colloids (Smith, 1926; Malowany and Newton, 1947).

(d) The steaming of some soils makes available more calcium, potassium, phosphorus, zinc, copper and nitrogen, according to Milliken (1942). Bad effects, which sometimes result from soil treatment, can not be attributed to this greater availability of these elements nor to that of aluminum, ammonium, iron or total salts, according to Robinson (1944).

Recent work has added many refinements to our basic knowledge but has also raised inadequately answered questions, some of which are related to the fact that soils rich in organic matter are very heavily populated with microorganisms. Thus in a study of the effect of steaming four different Canadian soils, Malowany and Newton (1947) found that soluble phosphates and sulfates increased by one-third in soils rich in organic matter. Capillary activity was reduced in all. No change in pH occurred, nor was there a change in particle size detected by mechanical separation. While steaming does not change the pH of the soil, the microflora that builds up after steaming an acid soil may be quite different from that which follows treatment of an alkaline soil, according to Herzog (1939) and Walker and Thompson (1949). Steaming a moist alkaline soil results in greater ammonia accumulation than a dry acid soil, which is probably the reason why adding lime to some soils before steaming may be detrimental (Walker and Thompson, 1949). Gypsum is much better, according to Hoffman (1939). Some soils contain replaceable manganese, and when other salts are present in abundance, steaming, particularly acid soils, may result in the accumulation of excessive amounts of water-soluble manganese, which is phytotoxic (McCool, 1934). Addition of lime to acid soils before steaming reduces the danger of toxicity from soluble manganese but induces faster ammonification. Addition of commercial fertilizers containing phosphates, particularly gypsum, reduces phytotoxicity from accumulations of both manganese and ammonium salts.

The microflora that follows steaming varies qualitatively and quantitatively for different soils, but *Trichoderma* seems to be one of the first to reenter and build up. Ludwig and Henry (1943) attribute to the activity of this fungus the unique fact that when *Ophiobolus* is reintroduced into steamed soil, it is less virulent than when introduced into non-steamed soil. Tam and Clark (1943) found that steam alone, chloropicrin or formaldehyde, or steam in combination with chloropicrin or formaldehyde eliminated nearly all the fungi except *Trichoderma* in a pineapple soil of Hawaii. Six weeks later a large population of both bacteria and Actinomycetes had developed in the soil. That some Actinomycetes can withstand steaming for many hours was shown by Kurzweil (1943). All the fumigants used by Tam and Clark inhibited

nitrification, and ammonia accumulated in proportion to the efficiency of the fumigant at killing the nitrifiers. Nitrification was repressed longer by steam than by chloropicrin and least by formaldehyde.

That annual treatments of soil have little permanent effect in altering the microflora is indicated by the study of Cohen (1950) on the effect of burning over and grazing the veld of South Africa. Seven years of burning did not result in a change or in the establishment of a distinct soil flora, though others have shown that cultural practices could do just this.

The delicate balance between nutrients and antibiotics that may exist in a given soil is illustrated by the work of Lambert and Humfeld (1939) who found that heating certain mushroom-casing soils, if the temperature goes over 135° F, may cause a reduction in the mushroom yields by 50 per cent. A somewhat similar situation was described by Lawrence and Newell (1936), where steaming a compost soil for 30 minutes caused retarded growth of *Primula simensis,* but steaming the peat, sand and loam ingredients of the compost individually before mixing, relieved the situation. However, Grooshevoy and Levykh (1936) obtained better results by mixing compost ingredients together before steaming. That there may be several types of injury resulting from heating of soil is indicated by Bewley (1950) who states that the control for one kind of injury may be flooding; for another, adding phosphate; and for a third, addition of horse manure. The first would eliminate excess soluble salts and organic matter; the second would presumably react and prevent accumulation of excess manganese; while the last would quickly alter biotic relationships and hasten the break-down of organic toxins.

In a comparison between steam and formaldehyde treatments, which, however, were not carried out to similar depths, made in a 25-year-old forestry nursery of high pH, Warcup (1951) found that more fungi recolonized the steamed soil and that fewer species recolonized the formaldehyde soil. The dominant recolonizer in the formaldehyde-treated soil was *Trichoderma virida;* in the steamed soil *Mortierella, Phoma* and *Coniothyrium* were prevalent. *Pythium* was recovered from both soils 13 weeks after treatment, and by the third year it was an abundant as ever in the steamed.

Work at the Pennsylvania Pasture Research Laboratory showed that the adverse growth effects of heating a soil are products of time and temperature. A few days at a temperature of 50° C produced the same toxic effect that two hours at five pounds steam pressure did (105° C?). The toxic effects were counteracted by applying an abundance of phosphate either before or after steaming, but were also removed by adding untreated soil to the steamed soil, according to Robinson (1944). In this connection the work of Winter is of interest. He found the runners of *Ophiobolus graminis* to be stimulated by treatment either with steam or with volatile fumigants, a fact he explained as due to the destruction of inhibitory factors by the soil treatment. These factors were restored by adding untreated soil, provided this was of a type similar to the original soil. The inhibitory substance produced by the microflora of one soil may be quite different from that of another. Thus a heath humus was very effective, while a loess was not. The complexity of these biotic factors is further indicated by the work of Meredith (1944) who, in a study of 66 soil samples in Jamaica, found 17 organisms out of 128 isolated that were able to retard the growth of *Fusarium oxysporum* in soil solution agar cultures. However, some of these were unable to retard this fungus if transferred to soil solution cultures prepared from other soil samples than the one they originally came from. Just what are these inhibitors?

Since fumigation is performed at ordinary soil temperatures and, therefore, does not break down organic matter and liberate soluble salts to the extent that steaming does, we can expect fewer toxins to be produced by soil fumigation, other than the lingering of the fumigant itself. Few people adhere to the dogma that fumigation benefits are attributable to chemical changes in the soil. Most investigators credit the value of soil fumigation to suppression of disease-inciting organisms. However, the biotic balance may be upset by fumigants almost to the same extent that it is by steam. In all cases nitrification is inhibited and ammonification accelerated. Thus Kincaid and Volk (1949) found a prolonged retention of ammonia in Florida soils fumigated in September, December and February with D-D and with ethylene dibromide. This extended into April with ethylene dibromide and into May with D-D mixture.

There is considerable specificity exhibited by some fumigants against certain nematodes. For example, Graham and Holdman (1953) report only half as many meadow nematodes (*Pratylenchus*) killed by a dose of ethylene dibromide which killed all the sting nematodes (*Belonolaimus*). Ethylene dibromide is believed by Gerald Thorne to be much more specific than D-D against the potato rot nematode (*Ditylenchus destructor*), while D-D mixture has been found much more effective against the golden nematode on Long Island, according to Lear et al. (1952). The resistance of the cyst stage of any nematode is greater than that of the egg, and of the half grown larvae than that of the mature larvae. So after a job of fumigation, if the full grown larvae of saprophagous nematodes are still found, it is pretty certain that the more resistant egg stages of parasitic nematodes have survived the treatment. Similarly, of 10 or 12 important soil fungi, the Pythiums and the Phytophthoras are much more susceptible to fumigants in general, and those with mild fungicidal properties in particular, than are, for example, the Fusaria (Zentmyer and Kendrick, 1949). The sclerotia of most fungi are harder to kill than the vegetative stages, especially when they are dry, but *Streptomyces ipomoea* was not controlled by dosages of D-D that did control *Sclerotium rolfsii* in Louisana (Martin, 1953).

We are still using the Edisonian method of testing soil fumigants and are very much in the empirical stage of correlating fumigation capacity with chemical constitution or molecular configuration. To some extent the toxicity of a homologous series of compounds is directly related to the boiling point, but, on the other hand, toxicity is also related to volatility in many cases; sometimes it may be the toxicity of the substituted radical used in raising the boiling point that is responsible for the effect. In general, the halogen radicals seem to be more fungicidal than the nitro, amino or alkyl substituents, according to Beraha and Powell (1953). With insects, which must respire to take up the fumigant, inherent toxicity as well as volatility are important. It is significant that chloropicrin, which boils at 112° C, is so much more toxic per unit than carbon disulfide, which boils at 46° C, that it is a superior soil fumigant. The work of Lehman (1942) is of special interest here. He tested 114 compounds and determined the median lethal concentration of 57 for wireworm control under

laboratory conditions. Of nine compounds which were more effective than carbon disulfide in the air, only three were more toxic than carbon disulfide in soil, and the relative toxicity of all substances was reduced in contact with soil, presumably by adsorption of the gases. The rate and extent of diffusion may be very important because chloropicrin, which in these laboratory tests was 14 times as toxic as carbon disulfide in air, was only three times as effective in the field. Similarly allyl isothiocyanate, which was 29 times as toxic in air, was just equal to carbon disulfide in field tests. The more rapid diffusion and lower adsorption of carbon disulfide are assumed to be responsible for its better showing in these cases.

Besides toxicity to the pathogen, phytotoxicity must be considered in evaluating a soil fumigant. Three factors are important here: the vapor pressure, the amount required to kill the pathogen, and the concentration tolerated by the host plant. Since volatility is negatively correlated with boiling point, the latter is a good criterion of the behavior of a fumigant with respect to the need for sealing it in and to the time required to get rid of it again. Fumigants that boil between 40° and 100° C will doubtless need a seal of some kind to permit building up to lethal concentration in the top two inches of the soil, but will escape rapidly. Those boiling between 100° and 120° C will not persist too long and may not need much sealing, while those boiling at 130° to 140° C need no seal as a rule, but may persist a little too long sometimes (Stark and Lear, 1947). Fumigants with extreme toxicity may be used at such low dosage rates as to offset their undesirable persistence. Ethylene dibromide falls in this class. It is even being used as a side dressing along the row against nematodes on pineapple and even beets (Curzon, 1951). Weak toxicants like xylene, on the other hand, even though of a low order of phytotoxicity, have to be used at such high dosage rates as to require long aeration periods. A product like methyl bromide is of special value for having high toxicity, low phytotoxicity and a high volatility, thus saving growers much time. But when cost also enters the picture, the ideal soil fumigant has not been found yet (Newhall, 1946). It should be highly toxic to a wide variety of pests but not too phytocidal or too persistent. It should be inexpensive, stable and not too disagreeable to handle or too hard on the equipment. No

wonder we are settling for a number of different fumigants, each with but a few of these qualities.

SUMMARY

The primary object of soil treatment, whether by heat or by volatile chemicals, is to kill pathogenic microorganisms, although many scientists at the beginning of this century were inclined to explain favorable plant responses chiefly on the basis of chemical changes and increased fertility.

In parts of the world the heat of the sun kills some pathogens, particularly root-infesting nematodes, the thermal death points of which are low. Surface burning and roasting of seedbed soils have been practiced for nearly a century and may have been common in ancient times.

Steaming is more effective than drenching with hot water, and has reached its highest state of development in greenhouses of the north temperate zone. A number of ingenious ways have been developed by growers to conduct steam to the soil. Among these are the buried perforated pipe, the buried tile, the inverted pan and the steam rake. A modification of the pan system, called the " surface system ", was found to work at low steam pressures. The relative costs of labor versus equipment usually determine which system a greenhouse grower adopts. The amount of coal required to steam an acre is in the neighborhood of 40 tons. The so-called merits of high pressure steam versus low, and of long time steaming versus quick pasteurization, are exploded myths. Less injury to rich soils is likely from the latter.

Electricity has been used to heat soil in two ways, one a direct heating system in which the current passes through the soil between two or more vertical or horizontal electrodes, the other an indirect process in which heat is imparted to the soil by thermal conductance from buried heating elements of uniform fixed capacity. Each has its good and bad points, but electric pasteurization is limited by the relatively small amount of current available to growers at any one time.

Flood-fallowing has specialized uses against some insects and fungi but requires such a long time and is available to so few growers that its adoption is restricted to a few special locations, as in delta regions.

Soil fumigation is one of the oldest and newest ways of successfully fighting soil pests. It reached a high state of development in Europe near the close of the last century where carbon disulfide was used on hundreds of thousands of acres in the fight against the Phylloxera of grape. After the first World War the merits of the war gas chloropicrin revived interest in this method. Other volatile fumigants began pouring from the organic chemical laboratories, and it has now become profitable to treat two or three hundred thousand acres of farm land devoted to tobacco, vegetables, pineapple and ornamentals in the United States.

The four most popular soil fumigants are ethylene dibromide, the dichloropropene-propane mixture known as D-D, chloropicrin and methyl bromide. Each has its place, but none is ideal. The least expensive are good, chiefly against nematodes and insects, while those with fungicidal properties, in addition, are more expensive. A number of others have not been quite good enough to gain great popularity.

The advantages from soil fumigation have been made possible through the development of inexpensive equipment for accurately dispensing metered amounts of the fumigants, often as little as three gallons an acre. Tractor-drawn equipment capable of doing many acres a day is now available.

Reducing losses from several root rot complexes by treatment with nematocidal and insecticidal fumigants has awakened people to the importance and widespread occurrence of many root-feeding nematodes and wireworms which help initiate fungus rots.

Formaldehyde has been used as a drench, a dust and a concentrate, and for small quantities of soil is very useful against fungus pathogens.

With the manufacture of over 1000 new organic chemicals a year by each of several manufacturers, there is every chance that some day better soil fumigants will be available. Several new ones are undergoing tests in various field laboratories all the time. We are still in the empirical stage of testing, although the boiling point is known to be important and the halogen substituents are more fungicidal than the nitro, amino or alkyl.

A good deal of specificity is known with respect to the toxicity of a given chemical for different organisms. The ideal soil fumigant is yet to be found.

Repeated annual fumigations have no deleterious cumulative effects over a five-year period, although temporary suppression of nitrification occurs for a few weeks as it does after steaming, with its attendant accumulation of ammonia.

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STUDIES OF MINERAL NUTRITION BY USE OF TRACERS

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INTRODUCTION

A completely satisfactory arrangement for grouping papers into topics for this review has not occurred to the writer; consequently the system employed may seem rather arbitrary. An attempt has been made to show the relevance of each paper to the solution of particular problems, wherever possible, hence the headings " absorption " and " translocation "; but when the topic of metabolism is encountered it will become obvious that only disjunct contributions are offered. In this area plant physiologists can show progress with only two tracer elements, i.e., phosphorus and sulfur, and even here metabolic patterns are hardly mentioned. Most of the work is still best described as " geographic tracing " rather than as true " metabolic tracing ". The other headings, " introduction ", " procedures " and " radiation injury ", are self-explanatory. The writer's justification for the omission of review type articles, of

which there were countless numbers in the early days of tracers, is that the useful parts of them are now adequately covered in textbooks.

The basic requirement of a tracer is that it be " chemically and physically exactly equivalent to the substance it represents or displaces and that it in no appreciable way affects the system differently from its normal counterpart " (Siri, 1949). Many of the radioactive tracers successfully fulfill these requirements, but this condition is not altogether satisfied with H^3 as a tracer for hydrogen or C^{14} as a tracer for carbon. Beyond this atomic weight the difference between the behavior of the radioactive isotope and the naturally occurring isotope is so small as to be negligible. For instance, the process of diffusion and the rate of reaction will be influenced by the mass of the isotopes quantitatively as $\dfrac{1}{\sqrt{\text{density}}}$; hence a rather wide difference in masses is required before the effect is large enough to be measurable. Heavy water (deuterium) is known to have a toxic effect and hence behaves differently from ordinary water (Barnes and Jahn, 1934). A differential effect in favor of one isotope over another has been noted for carbon and oxygen isotopes (Kamen, 1946), but it is with tritium that the greatest isotopic effect is to be expected.

The processes of diffusion and metabolism, in a single cycle through a plant, do not affect an isotopic separation of any magnitude for elements of higher atomic weights. Mullins and Zerahn (1948) have examined the K^{40} content of potassium from animal, vegetable and mineral sources, and compared it with reagent KCl. No difference in K^{40} content within $\pm 0.5\%$ could be demonstrated. A number of cases were cited in the above reference wherein an isotopic separation had been reported (for *Valonia* and *Nitella;* see Jacques, 1940).

It has been shown (Vinogradov and Teis, 1941) that H_2O^{16} and H_2O^{18} are used indiscriminately in photosynthesis and that the O_2 produced in photosynthesis comes from the water (Rubens et al., 1941). Therefore neither isotope of oxygen is favored in oxygen production; however, the heavier isotope of oxygen may react more slowly in respiration, as has been suggested by Rabinowitch (1945) to offer a probable explanation for the observation that atmospheric oxygen is about 7.5×10^{-5} atomic weight units heavier

than the oxygen in water of the oceans (Swartout and Dole, 1939). Cycling through many plants during many ages may have affected an appreciable isotopic separation.

The C^{12}/C^{13} ratio of 105 plants representing all major plant groups has been determined by Weakman (1952). With the possible exception of Gymnosperms, there appeared no systematic differences between groups. The local carbon dioxide cycle, however, was responsible for some variations between individuals.

Radioactive tracers may also affect biological systems differently from normal elements in that they emit ionizing radiations which are responsible for the production of molecular fragments of protoplasmic constituents. However, this review will concern itself only with those cases where attempts have been made to establish a threshold involving the first injury to some physiological process. When radioisotopes are used in what is commonly called " tracer amounts ", the biological effects of the radiation are frequently disregarded because of the smallness of the effect. However, as more refinement is attained, it may be necessary to revise our concepts as to the threshold value wherein a radioactive tracer first alters a physiological process. (See Mackie et al., 1952.)

According to Hevesy (1948a), by whom the first use of tracers was made, the historical background for this type of study dates from the attempts made in Rutherford's laboratory to separate the radium D embedded in the lead obtained in the separation of radium from pitchblend. Failure in 1911 and 1912 to effect a separation led Hevesy to find a use for the unseparated material. This he and Paneth, after similar failure, used to determine the solubility of lead salts, and later with Zechmeister (Hevesy and Zechmeister, 1920) to show that lead in lead salts did not interchange with lead ions in solution. Organic lead compounds showed the same absence of interchange. Hevesy (1923) then used this material to follow the uptake of lead by plants.

Later work has shown that neither labeled phosphorus (Hahn and Hevesy, 1940) nor sulfur (Tuck, 1939) interchanges when brought together with organic compounds present in organisms. This, however, is not true of hydrogen bound by oxygen or nitrogen (Reitz and Bonhoeffer, 1934). As it would have been impossible to advantageously use as a tracer any atoms which randomly exchanged positions with other atoms in organic combina-

tion, it was of fundamental importance to establish the fact that physical interchange did not occur.

With this basic fact established, it became practical to introduce marked atoms into any biological system which could be sufficiently isolated for study and to follow the normal course of reactions throughout the process. This technique allows discernment of the experimental atoms from those initially present in the organism and permits one to follow the " growth " of these particular atoms into or through any given system. With this method a new, or at least a much more dynamic, view of the " turnover " of atoms and molecules within living systems has resulted. The concept that the materials taken in do not pass through and become exhausted as wastes, but instead that they enter into the structure of the organism as they are metabolized, persist there for a characteristic period and then become discharged to make way for more recently acquired materials, is a basic concept of biology which has come to full realization by the use of tracers.

True, there were adherents to this view prior to the widespread use of tracers, but the concrete evidence for the extent of turnover and the quantitative expression of turnover rates, especially the exact mechanisms of turnover, have been acquired only recently. The realization that such a dynamic system exists is a basic contribution to the fundamental concepts of biology.

Among the advantages of the tracer methods is the ability to identify one's experimental atoms from all others and to follow them in their geographic wanderings or through their various chemical combinations. A similar advantage is the minuteness of the number of atoms that can be so followed. A few thousand atoms can easily be detected and quite accurately measured in a quantitative sense (DuBridge, 1938).

The disadvantages are related to the advantages. If such a few atoms can be detected, they can, if carelessly handled, contaminate samples and render determinations uncertain. A whole new standard of laboratory cleanliness has emerged and has attained a level of perfection, even above that employed in the handling of pathogenic organisms. The pathogenicity of an organism can be destroyed by heat—radioactivity is a physical property of the atom and as such remains unaltered, except by its characteristic natural decay. In the homely process of washing dishes one must be ac-

tively concerned with the physical removal and proper disposal of the last atom. Another disadvantage is the effect of the radioactive emanations on the processes being studied; this will be treated in a later section.

When considering a procedure involving radioactive isotopes as a possible means to the solution of a specific problem, one must bear in mind convenience, rapidity and accuracy; and in addition, consideration must be given to the danger of spillage and contamination. One is often intrigued by the apparent rapidity with which assays may be made on a prepared sample with little regard to the laborious procedure of obtaining the sample. In their preparation extreme care must be exercised in guarding against contamination between samples and in contamination of the laboratory in general which would render it difficult to continue work without contaminating future samples. Health precautions must also be realized. Finally, disposal of the radioactive material in a proper way oftentimes presents definite problems. All of these considerations should be fully appraised before one attempts a solution of a specific problem by the use of radioactive isotopes [1]. After a number of years experience, it is generally conceded by most workers that if an answer can be obtained in some other way than by tracer methods, the labor involved would not justify the latter. However, there are so many physiological problems for which a direct answer can be obtained only by utilization of marked atoms that this method should become a standard procedure in all physiological laboratories. Once the initial setup is in operation, the attack on specific problems becomes much simplified, and more problems can be justifiably attempted by this means. So many advances have been made by means of these procedures that it is no longer necessary to defend their use.

The amount of radioactive material which it is necessary to handle in tracer work presents no serious health hazard to an experienced user if reasonable caution is exercised. It is the opinion of the writer that improper handling of radioactive materials in

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[1] A number of pamphlets on health precautions and procedures are available from the Technical Information Division, U.S.A.E.C., Oak Ridge, Tennessee. Two handbooks by the National Bureau of Standards, i.e., *Safe Handling of Radioactive Isotopes* (Handbook 42) and *Control and Removal of Radioactive Contamination in Laboratories* (Handbook 48) are available through the Superintendent of Documents, Washington 25, D. C., for 15 cents each.

tracer amounts will render measurements unreliable and the laboratory useless as a working place prior to the time that health considerations become a serious factor.

<div align="center">PROCEDURES</div>

✓ Since the time of Becquerel (1896) it has been known that radioactive materials possess the important property of discharging electrified bodies. Rutherford (1899) found that this discharging action could be explained on the assumption that the gas was ionized by the passage of the radiations through it. Mme. Curie (1898) employed a suitable electroscope to measure the ionization produced by radioactive bodies. Based on these principles, but at a later date, the now familiar Geiger-Mueller (1928, 1929) counter was devised. These fundamental procedures have lately been employed together with elaborate recording circuits for the accurate measurement of radioactive substances.

The standard textbooks on radioactive tracers now serve as a general outline for the common procedures employed in biological studies (Hevesy, 1948b; Siri, 1949; Kamen, 1951). There are, however, several articles covering specialized techniques which may be worthy of mention here. Radin (1947, 1948), in a series of five articles, has presented a comprehensive treatise of methods, backgrounds for methods, and basic concepts. The general philosophy of tracer uses is presented. Cohn (1948) has given a discussion on the origin of contaminants in radioisotopes together with methods of detection and removal. Yankwich (1949) has covered errors, isotope dilution analysis, purity and isotope effects. Instrumentation has been discussed by Borkowski (1949) who included Geiger-Mueller counters, proportional counters, ionization chambers and electroscopes, and gave a comparison of counting rates for the different devices. Measurement techniques are reviewed by Kohman (1949) in a discussion of sample preparation, sample errors, instrument errors, absolute measurements and statistical considerations. A discussion of radioactive tracers in plant nutrition has been presented by Martin and Russell (1950). Their article covers the chemical and physical behavior of isotopes before disintegration, the effects of the new substances formed, and the effects of the radiation they emit. The general value of tracer

methods is also considered. Most of the above topics also receive attention in the standard texts.

There are instances wherein the use of tritium in marking water would seem desirable. The techniques for measuring tritium are somewhat more complex and involve the decomposition of water and determination of tritium as gaseous hydrogen. Several procedures have been outlined. Henriques and Margnetti (1946) describe a procedure based upon the insertion of hydrogen gas in a quartz ionization chamber attached to a Lauritsen electroscope. Robinson (1951) caused radioactive water to react with methyl Gringard reagent to give radioactive methane which was emitted in a proportional counting chamber. Libby presents procedures and theories for C^{14}, S^{35}, T and others (1947), and in later articles Grosse et al. (1951) and Wolfgang and Libby (1952) describe a procedure for determining tritium based on the decomposition of water by zinc and the introduction of the hydrogen sample into a Geiger-Mueller tube with ethylene and argon as counting gases. The writer has used this procedure to advantage where small bits of tissue are to be analyzed. There is some question as to the value of tritium as a marker for water. The isotope effect should be maximum here and render the behavior of radioactive water slightly different from normal water in biological systems. Before employing this method, one should consider carefully whether an isotope effect will be a disadvantage in the procedure being contemplated. Wherever metabolic water is concerned, the isotope effect is to be expected, as it also is in absorption, a process involving diffusion.

There are some instances wherein an " in vivo " assay of radioisotopes in plants is highly desirable. This would be particularly advantageous on expanded organs such as leaves or on stems where rates of movement are to be determined. Pace et al. (1948) have presented a design for a small Geiger-Mueller tube to be used with gamma emitters. Klechkovskii, Tselishcher and Evdokimora (1951) have used shielded counter tubes for determination of radioactivity in leaves, and Martin (1952) has developed a switching device in order that four G-M tubes could be successively fed into one scaling circuit. The assay of fresh tissue in place should also prove most valuable as a pilot method for determining the ap-

pearance of radioactive materials in tissues prior to an accurate analysis either by direct counting or by autoradiographic preparations.

DIRECT COUNTING. Direct bombardment of tissues in a pile is a possible way of inducing radioactivity in certain trace elements, i.e., those with a sufficiently large " cross section ", to readily effect neutron capture at the flux employed. Tobias and Dunn (1949) show a typical distribution of radioactivity obtained together with the decay characteristics.

Direct assay of radioactivity in solutions has appealed to a number of investigators, and several systems for conducting such analyses have been offered. It should be pointed out, however, that the majority of investigators are using counting procedures based on solid or gaseous samples. A dipping counter tube has been described by Bale et al. (1939). Smith and Cowie (1941) describe methods used in preparing standards and in determination of C^{11} in liquid samples. McAuliffe (1949) describes a rapid method for P^{32} determination in solutions which flow around the sensitive portion of the G-M counter, in which he claims an accuracy to one per cent. Schweitzer (1949) compares three methods of measuring radioactivity in solution: open solution counting allowed detection of the lowest energy particles; the enclosed solution method was the safest; and the dipping counter method was the least efficient. Freedman and Hume (1950) describe a method of covering liquid samples with lacquer so that they may be used with safety under the window of a G-M tube. Fluids containing radioactive elements may also be dropped from a micropipette onto filter paper which can be dried and cemented onto a metal disk for " counting " (Burch et al., 1950).

A mathematical treatment of the possibilities of using isotopes to determine the rate of a biological reaction has been prepared by Branson (1947). This is an area into which biologists should attempt an invasion. Fundamental treatments of the theory of rate of reaction can be found in physical chemistry literature.

Special care must be exercised in handling radiophosphorus because of its tendency to adsorb onto glassware. In order to avoid this difficulty, Hall and MacKenzie (1947) used dimethyldichlorosilane (a precursor of silicone) to coat their pipettes, graduated

cylinders, centrifuge tubes, etc. Several commercial preparations are available for this purpose. Several sets of glassware were coated, as there was a tendency for abrasion, dust and grease to cause the coated surface to lose its hydrophobic characteristics. Vessels of different kinds were also treated with butyl methacrylate.

In preparing samples for analysis, MacKenzie and Dean (1948) found it advantageous to convert phosphorus to $MgNH_4PO_4 \cdot 6$ H_2O. This material was filtered onto a suitable holder so that P^{32} and total phosphorus could be determined on a single preparation. In addition, they offer a number of suggestions concerning the use of G-M counters and counting conditions.

The desirability of counting compressed plant material directly in order to avoid the lengthy chemical procedures necessary to obtain purified precipitates has led MacKenzie and Dean (1950) to develop a procedure of converting plant material into briquets and determining the activity of the compacted material directly. After standardization of their procedure, specific activity could be calculated from measured activity and a total phosphorus determination on a portion of the sample. This procedure is particularly desirable when a large number of crop plants must be surveyed in the shortest possible time.

The assay of radiosulfur presents some difficulties which are not serious with radiophosphorus. The former is frequently assayed from a preparation which is infinitely thick with respect to the path of the emerging electron in the sample (Hendricks et al., 1943), while the latter is more often " counted " as a " thin " preparation. Use of a " flow counter " for S^{35} makes possible the use of thin samples if the amount of material necessary for the assay can be spread infinitely thin with respect to the path of the electron in the sample material.

It is sometimes desirable to introduce a radioactive isotope into plant material which is to be used in feeding studies involving animals. It is then desirable to know how to acquire the highest possible activity in the particular plant fraction to be used. This involves a knowledge of the absorption and translocation characteristics of the element in the plant in question. Jacobson (1948) describes a procedure for introducing radioactive phosphorus into the grain of growing corn. He found it advantageous to introduce the radioactive phosphorus into the nutrient solution when the

corn was in the early milk stage of kernel production. The mature corn grain then had the highest radioactivity of any part of the corn plant. Sufficient radioactivity in the grain was obtained for satisfactory feeding experiments with poultry. Using the same principle to a different end, White, Fried and Ohlrogge (1949) showed green manure containing P^{32} to be as effective a source of phosphorus to plants as potassium dihydrogen phosphate on a phosphorus-deficient soil.

AUTORADIOGRAPHY. Although the fact that radioactive materials would affect a photographic plate was discovered by Becquerel in 1896 and the first autoradiographic studies were made as early as 1904 (London, 1904), the autoradiographic technique was not widely used until pile-produced isotopes became available. The whole tissue technique for the preparation of autoradiographs can be easily mastered by anyone who has some knowledge of dark-room procedures. The quality of the radiograph will depend upon a number of factors, namely, the energy of the particle emitted by the radioactive material (the lower energies resulting in the highest resolution), the degree of contact between the plant material and the film, the choice of film, and the choice of the proper exposure time. Care must be taken to protect the film from contacts which would cause it to blacken as a result of chemical reactions (Boyd and Board, 1949). No-screen x-ray film has been most widely used for this gross type of autoradiograph, since it combines speed with a maximum silver halide content. Rediske and Biddulph (1953) found it suitable for such weak emitters as Fe^{55}. A procedure for simultaneously preparing a number of autoradiographs has been described by Wittwer and Lundahl (1951).

The gross radiographic technique provides an expedient tool for the study of absorption, translocation and distribution of various elements in plants. Arnon, Stout and Sippos (1940) traced the metabolism of inorganic phosphates in the leaves and fruits of tomato and found that the younger the fruit the greater the capacity for phosphorus absorption, although fully ripe fruits still attached to the plant continued to accumulate small amounts of phosphorus in the pulp. Colwell (1942) applied radioactive phosphorus to squash leaves and studied its translocation to other parts of the plant by means of autoradiographs. Harrison, Thomas and Hill (1944) were the first to use sulfur autoradiographs and

showed the distribution of this element in wheat. In a particularly striking report Sayre (1952) made a systematic study of the differential accumulation of 14 radioactive elements in the leaves of corn plants. Zinc nutrition of the tomato vine grown from germination to maturity with all the zinc tagged by Zn^{65} was studied by Stout et al. (1947). They found a greater portion of the zinc in seeds and conducting tissues than in the pulp of the fruit. They also noted that the abscission tissue on the stem of the fruit absorbed more zinc than the stem above or below this area. Grosse and Snyder (1947) have published autoradiographs of geranium leaves which had been exposed to an atmosphere containing C^{14}. Translocation studies of a number of elements in red kidney bean have been carried out by Biddulph (1951, 1953) and by Rediske and Biddulph (1953) who used iron and phosphorus to study absorption and translocation in this plant.

Out of this gross autoradiographic technique has grown a more refined or histological technique wherein an attempt is made to correlate the source of radiation with an exact locality or tissue within the plant. The number of difficulties encountered in this new method has resulted in many studies to obtain a more precise localization of the radioactive isotope with respect to the film. One of the major problems has been to develop a suitable emulsion —the ideal one having small grain size, a high and uniform silver bromide content and speed, a combination difficult to obtain. In addition, it has been necessary to develop extremely thin emulsions which can be closely applied to the tissue section and which have a selective response to the different types of radiation. Track emulsions have helped to alleviate the difficulty caused by " spread " of the activity in the emulsion due to the discharge of particles in all directions from the isotope.

There are other attendant difficulties in the preparation and mounting of tissue without loss of soluble tracer and in the incorporation into tissue without injury of enough isotope to give the large radiation intensities needed for proper exposure of the film. The only practical way to avoid loss of soluble tracer from tissue seems to be by freeze-drying (Holt, Cowing and Warren, 1949). Freeze-drying is also indicated when rapid decay of the isotope would make conventional tissue preparation impractical. At present this technique has been more extensively applied to animal

tissue than to plant tissue. According to Boyd and Levi (1950), the problem of getting images without incorporation of such large amounts of isotope into the tissue is partially solved by the newer β-track films.

The basic problem, that of getting a close correlation of image and section so that there is a precise localization of the radiation source, has been approached in a number of ways. The first method tried was to clamp the mounted section to the emulsion side of the photographic plate which was later developed. In this case the autoradiograph could not be observed in direct relationship to the histological section which produced it. To meet this difficulty Belanger and Leblond (1946) poured a melted emulsion over the section, and Pelc (1947) covered the section with a photographic emulsion stripped from a photographic plate. Some workers have mounted the histological section directly on the emulsion (Evans, 1947; Bourne, 1952; Russell, Sanders and Bishop, 1949; Endicott and Yagoda, 1947). Most recently Gomberg (1951) has gone back to the wet-celloidin photography of the 19th century and has evolved a process of emulsion formation over the histologic section mounted on a slide. The process is believed to extend to about one micron the resolution possible with weak beta emitters.

Microautoradiography has been much more extensively used with animal tissue than with plant tissue. Since the method is a new one, even these papers deal principally with techniques (Duggar and Moreland, 1953). Howard and Pelc (1951) have demonstrated the nuclear incorporation of P^{32} in the roots of *Vicia faba* seedlings. They found indications that incorporation of phosphorus stops sometime before visible prophase and does not occur during the actual division. From their autoradiographs, Russell, Sanders and Bishop (1949) concluded that the concentration of phosphorus in young barley plants occurred especially in the apical meristem, the leaf primordia, the bases of the younger leaf sheaths and initials of adventitious roots.

The development of the phase microscope has made the study of unstained sections practicable. Removal of paraffin from the section and superimposition of a sensitive emulsion complete the tissue preparation. After exposure and development the combined tissue section and autoradiograph can be studied together.

ABSORPTION

The literature on absorption problems was voluminous and the topic a lively one for investigation prior to the widespread use of " tracers ".   However, when applied they materially aided in a clear resolution of absorption problems into surface exchanges and metabolic uptake.   Although the duality of the phenomenon was quite generally recognized prior to that time, the tracer method, by its ability to differentiate the experimenter's " probe " atoms from the cell's general atomic complex, facilitated in obtaining a clearer expression of the idea.

Radioactive lead was first used to attack permeability problems (Hevesy, 1923).   By this means it was shown that lead atoms associated with roots remain replaceable by other lead atoms, hence are not in organic combination.   It was shown (Lark-Horovitz, 1929) that lead ions do not readily enter the sap of the living cell but will penetrate dead cells readily.   Radon, however, distributes itself evenly between cell sap and the bathing solution. Hevesy, Linderstrom-Lang and Nielson (1937) used phosphorus to determine the exchange between phosphorus atoms of yeast cells and those of the nutrient solution.   They found that yeast did not exchange its phosphorus.   Their views were that phosphorus was either present in organic combination and hence not exchangeable or that the cells in the mature state were impermeable to phosphate ions.   Mazia (1940) summarized his views on the binding of ions by the cell's surface.   He pictured the cell's surface as simultaneously a barrier and a reservoir for ions.   The binding of ions in the surface, in general, prevented their penetration into the interior. There appeared, however, conditions under which the bound ions might be released into the interior and might set into motion far-reaching changes.

Spiegelman and Reiner (1942) presented a mathematical treatment of the problems of permeability, and as a result suggested that chemical forces, as distinguished from electrical, should provide a more fruitful approach to the problems of potassium and sodium balance within cells.   Holm-Jensen et al. (1944) derived formulas for expressing diffusion constants in cm./hr.   They showed that permeation resistance is mainly in the outer protoplasmic membrane; the inner is responsible for a few per cent at most.   They hold that concentration differences within and without a cell are

maintained as a steady state phenomenon. Krogh (1946) reviewed the problems of permeability and exchange, and presented a method of distinguishing between active ion uptake and passive permeability. A formula for expressing permeability in centimeters per hour was included.

Brooks (1937, 1938a, 1938b, 1938c, 1939, 1940) undertook a study of selective accumulation in relation to permeability and was able to trace migration from the bathing solution across the cytoplasm to the vacuole. He visualized potassium as moving in combination with protein constituents. The initial stage of uptake was regarded as being an exchange reaction (for non-isotopic potassium). This was followed by a steady intake in some way related to metabolic processes. The first stage of uptake was later referred to as " induced accumulation " which appears to be an exchange phenomenon. This state is followed by " primary accumulation " which seems to be related to the metabolic accumulation later referred to by Hoagland (1940). The relationship of the exchange reactions to other substances was studied by Mullins and Brooks (1939) and Mullins (1941). The technique used in these studies was that of following the outgo of the labelled element from cells to the bathing solution, the bathing solution containing the elements which were tested for their effects on permeability. The rate of loss induced by the test elements followed the Hoffmeister series. Rubidium was the fastest and lithium the slowest in replacing potassium. For sodium, the Hoffmeister series was reversed. Very little loss occurred to distilled water. They furthermore showed that recently absorbed ions were more easily replaced than those acquired earlier. This was due to the probable absorption of radioactive tracers on the protoplasmic granules (Mullins, 1940).

The magnitude of the binding capacity of tissues was shown by Mazia and Mullins (1941). They immersed *Elodea* leaves in very dilute solutions of radioactive copper chloride and found that the cells were able to accumulate copper in excess of 3×10^8 of that present in the nutrient media. Mullins (1947) showed the rapidity of movement of substances within single cells of *Nitella* and *Chara* by dipping the ends of the cells into a solution containing radiophosphate and tracing movement by autoradiographic procedures.

Phosphorus uptake by yeast cells was shown to be almost entirely dependent upon carbohydrate metabolism (Mullins, 1942).

It was found possible to increase the radioactive phosphate exchange by yeast in the presence of glucose by the addition of trace amounts of riboflavin to the suspending medium. The increase observed ranged from 20 to 200 per cent over the phosphate exchange by controls using glucose alone. The presence of a phosphorus complexing factor at the cell's surface was shown by Nickerson and Mullins (1948).

The concept of base exchange, a problem directly in the realm of mineral nutrition, was also attacked with radioactive tracers. For many years it had been generally believed that exchanges of certain mineral nutrients between soil colloids and plant roots take place, but inability to distinguish atoms of one system from those of the other made it impossible to demonstrate it conclusively. Jenny and Overstreet (1939a, b) showed the extent of such an exchange and proposed a theory of contact exchange in which cations may transfer from clay to root and vice versa without entering the soil solution. These two authors with Ayers (1939) state further that " theories of chemical soil solution no longer suffice to explain fully the absorption of mineral elements by plants from soils. They must be supplemented by considerations of contact effects ". The rationale of the work by this group is presented by Overstreet and Jenny (1940). (See also Williams and Coleman, 1950).

Ions diffuse on the surface of colloidal particles and " jump " from one particle to another if the double layers interpenetrate. Roots may likewise participate (Jenny and Overstreet, 1939a). Overstreet, Broyer, Isaacs and Delwiche (1942) then showed that synthesized organic acids—and not carbonic acid—are the source of the hydrogen ions which replace the absorbed K on the clay. Carbonic acid was not involved in the end results of the accumulation reaction—but its participation in an intermediate reaction was not ruled out.

Vlamis and Pearson (1950) observed that the presence of CO_2 in a leaching solution of H_2O, nutrient solutions, etc. did not release either zirconium or niobium from the soil, but the presence of organic acids did. This is cited as additional evidence that excreted CO_2 does not function directly in mineral uptake by aiding exchange. Complete solution of this problem or formulation of a related one (see below on ion binding substances) would aid materially in clearing up a long-standing uncertainty.

By 1940 Hoagland was able to summarize his views on the de-

pendence between salt accumulation and metabolic activity in roots (Hoagland, 1940). Others of his group (Broyer and Overstreet, 1940) showed exchange to take place, both surface and deep seated, during periods of active (metabolic) salt accumulation, and in 1942 Hoagland and Broyer (1942) showed that cyanide, methylene blue and anaerobic conditions all suppressed salt accumulation, and that vacuolar accumulation did not occur anaerobically.

In some experiments with carrier free Rb^{86} and P^{32}, Overstreet and Jacobson (1946) showed that non-metabolic rubidium uptake rapidly reached a limiting value, while P^{32} approached a constant rate of uptake. Outgo was similar to uptake. This non-metabolic uptake was to a large degree confined to the first few millimeters of the root tip. That maximum absorption of Sr^{85} and I^{131} occurs within a few millimeters of the root apex was shown by Jacobson and Overstreet (1947). Dead roots showed the same pattern but accumulation was lower, and exchange for inert isotopes was much more rapid. The presence of ion-binding substances in the living protoplasm was indicated.

In an attempt to explain the rapidity with which one ion can be ' displaced from roots by a chemically related ion, and in addition to explain the apparent competition between the absorption of related ions, Jacobson et al. (1950) have postulated that an ion-binding substance may be present at the surface of roots. Competition for space between ions of a related character could then be explained. Unrelated ions may be bound by different ion-binding substances. This suggestion seems an inevitable one and has occurred a number of times (Hevesy, 1947a; Jacobson and Overstreet, 1947; Nickerson and Mullins, 1948; Hendricks, 1953). It has intriguing possibilities in helping to explain competition between similar ions for absorption " space ".

Broyer (1950) used radioactive Br in a study with excised barley roots, and confirmed again a rapid exchange reaction between the external medium and roots, but showed it to be relatively less important than migration by metabolic accumulation under favorable temperature conditions. At low temperatures exchange absorption predominated with high salt roots, but with low salt roots metabolic accumulation was more important. The movement of bromide across the root appeared to take place by either of two pathways. In low salt roots the path may be to vacuoles and

xylem. In high salt roots it is largely to xylem via the proto-plasmic continuum. An exchange of phosphorus between root and nutrient solution amounting to 0.5 to 1.5% per day has been shown by Barbier and Husson (1952).

While excised roots have been of value in the study of certain aspects of the absorption problem, it does not follow that the in-formation so derived can be projected to determine the site of ab-sorption of the major fraction of the translocatable nutrients. As the study of the absorption mechanism matures, it is hoped that it will not be divorced from translocation, as this is the process which is responsible in a great measure for its continuation. Kramer and Wiebe (1952) have shown some departures from the view that the meristem is the principal site of mineral accumulation (specifi-cally for P^{32}).

The absorption of fertilizer elements under field conditions can be studied to very good advantage by tracer methods. The nutri-ent environment can be treated as one system and the plant as another. In practice the tracer materials are mixed with the in-digenous plant nutrients, the plants grown therein, and the plant parts then analyzed for both indigenous and tracer elements. This furnishes a basis for determining the efficiency of fertilizer uptake. This is a totally new approach to the fertilizer problem and offers the means for direct calculation of the percentage of applied element which makes up the final yield of plant material.

It is also likely that other methods of fertilizer application will become widespread. Particularly promising is the method of direct application of certain fertilizer elements to foliage. The feasibility of this method of application is based on the demonstra-tion of the free and rapid movement of phosphorus (Biddulph, 1941; Biddulph and Markle, 1944) and of sulfur (Thomas, Hen-dricks and Hill, 1950) in plants. Other elements which are phloem mobile should be equally effective when applied in this manner. The feasibility of this method for the application of phos-phorus has been recently demonstrated by Wittwer and Lundahl (1951), Silberstein and Wittwer (1951) and Eggert et al. (1952). The problem of a suitable method of application should present little difficulty.

The first work utilizing radioactive isotopes and dealing with strictly agricultural problems was completed by Henderson and

Jones (1941). They showed that P^{32} applied to the soil surface as $Ca(H_2PO_4)_2$ penetrated as little as one and one-fourth inches into a clay soil and four inches into a silt loam when washed down with water equivalent to two and one-half inches of precipitation. Only 5% of the K^{42} applied as KCl penetrated beyond one and five-eighths inches with the same addition of water. The authors conclude that " the radioactive technique appears to present a valuable method for studying the behavior of ions in soils ". This paper was followed immediately by Ballard and Dean's report (1941) that fixation of phosphorus in soils was much more tenacious than for sand cultures. Soil fixation approached that which was calculated by other means to be characteristic of phosphorus in the soils tested. Tomato plants were unable to utilize readily the so-called fixed phosphorus of soils, whereas Sudan grass was able to make some utilization of this fraction.

Comar and Neller (1947) developed radioactive phosphorus procedures for studies of soil fixation and uptake by plants of radiophosphorus distributed in soils; and Neller and Comar (1947) showed the fixation power of soils for phosphorus against a dilute acid extractant to be directly related to their clay contents. Fixation varied directly with the moisture equivalent but showed no correlation with pH values. MacKenzie and Dean (1948) have reported procedures and measurements for P^{31} and P^{32} in plant material. They included procedures for determining the specific activity of plant material containing radioactive phosphorus absorbed from P^{32} treated soils. By comparison of the specific activity of the fertilizer preparation with that of the plants grown on soil receiving this fertilizer, the proportion of the phosphorus contained in the plant which was derived from the fertilizer was estimated. This allows a calculation of the fertilizer efficiency under different modes of application and by different crops.

In 1946 the Canadian group began a series of reports, the first of which (Spinks and Barber, 1946) pointed out that " it is possible to measure the phosphorus taken up from both fertilizer and soil and the utilization of the fertilizer phosphorus, something which could not possibly be done by ordinary chemical means ". In 1947 they (Spinks and Barber, 1947) showed a seasonal variation in uptake of fertilizer phosphorus by wheat with highest uptake when the roots were still in the zone of application and lowest

uptake during later stages when the roots had spread beyond the zone where the fertilizer was applied. In their experiments the main uptake of fertilizer phosphorus took place prior to the heading out stage. Approximately 22% of the fertilizer phosphorus was recovered by the plant. The next year's results (Spinks and Barber, 1948) led them to believe that most of the phosphorus taken up in the early stages of growth comes from the fertilizer. In 1948 (Spinks, Dion et al., 1948) they reported that the amount of fertilizer phosphorus taken up increased with its application, but the per cent uptake decreased. Also fertilizer application results in less uptake of indigenous phosphorus, ammonium phosphate being used in these experiments. Dion, Spinks and Mitchell (1949) and Dion, Dehm and Spinks (1949) showed ammonium phosphate to be a particularly suitable carrier of phosphorus in the base-saturated soils of Saskatchewan. Mono-calcium and di-calcium salts gave decreasing effectiveness. A review of the above work has been published by Spinks and Dion (1949).

A study of phosphorus absorption by individual wheat and barley plants grown in test tubes has been reported by Naylor et al. (1951). An accounting of the deposition of the absorbed P^{32} by each part is included.

Meanwhile the U.S.D.A. investigators had been perfecting a system for the use of P^{32} in fertilizer studies, and their series of papers, published in 1947 (Hendricks and Dean, 1947; Nelson et al., 1947) furnishes a sound pattern for fertilizer studies with this element. A fertilizer is prepared with a known ratio of radioactive phosphorus to inert phosphorus. If a plant grown in soil to which this mixture has been added shows a ratio only one-fifth as great, then only one-fifth of the phosphate came from the fertilizer, the dilutant coming from the reservoir of indigenous phosphate in the soil. This " dilution " method is the basis of most fertilizer studies. It is " . . . so simple as to appear almost trivial, but it permits an entirely new approach to work with fertilizers ". Some results employing this method show that plants derive a higher percentage of applied fertilizer phosphorus from soils of low phosphorus fertility than from soils with high phosphorus fertility (Dean et al., 1947). Potatoes, corn, cotton and tobacco vary greatly in absorption of fertilizer phosphorus on soils of comparable native phosphorus content. Also the period of greatest absorption, whether early in development or later, varied with the crop (Nel-

son et al., 1947). Exchange reactions between phosphate on the surface of soil minerals with phosphate in solution were also followed (McAuliffe et al., 1947). The results from their 1949 experiments, including information on P^{32} absorption of potatoes, tobacco, corn, cotton, orchard grass, ladino clover, oats, alfalfa, sugar beet, wheat, barley and soybeans, are indicated as being tentative but tend to show that as roots grow through the fertilizer placement area the per cent of fertilizer phosphorus in plant parts decreases. Corn showed ten to 30% utilization of fertilizer phosphorus in early growth, falling to four to 15% by the roasting-ear stage (Stanford and Nelson, 1949a). In general the percentage of fertilizer phosphorus in the plant material was rather low, i.e., ladino clover 20% (Blaser and McAuliffe, 1949), potatoes four to 15% (Jacob et al., 1949) and cotton 5% on low phosphorus soils and 3% on high phosphorus soils (Nelson et al., 1949). Potatoes gave highest figures when compared under similar conditions to corn and soybeans (Krantz et al., 1949).

᠂ Banding or mixing the fertilizer with the soil (Woltz et al., 1949), especially at seed depth (Stanford and Nelson, 1949a; Nelson et al., 1949), was superior to broadcasting as a method of application. Drilled fertilizer was also superior to broadcasting (Blaser and McAuliffe, 1949). Deep placement was better than shallow (Olsen and Gardner, 1949).

Superphosphate appeared to give a higher percentage of fertilizer phosphate in plant parts than other forms including calcium metaphosphate, dicalcium phosphate and tricalcium phosphate (Blaser and McAuliffe, 1949; Hall et al., 1949; Stanford and Nelson, 1949b; Olsen and Gardner, 1949).

Another tendency was for the percentage of fertilizer phosphorus utilized by the plants to increase with the amount of fertilizer applied, especially in low phosphorus soils (Jacob et al., 1949; Woltz et al., 1949). That the application of fertilizer phosphorus increased yields and phosphorus content of plant parts was not always the case. Also included are studies on the utilization of farm manure labelled with radioactive phosphorus (McAuliffe and Peech, 1949; McAuliffe et al., 1949) and phosphorus uptake from green manure by rye grass (Fuller and Dean, 1949). (See also White, Fried and Ohlrogge, 1949.) These studies are the result of carefully planned experiments and, in general, show the possi-

bilities of applying tracer techniques to the general problem of fertilizer efficiency.

Fredriksson and Wiklander (1950) applied superphosphate containing P^{32} to a sandy loam soil low in available phosphorus. They found that both yield and uptake of fertilizer phosphorus increased with the amount of phosphorus supplied. At high rates of application, broadcasting gave better yield than placement beneath the seed. Collier (1951) and Low (1951) have presented general reviews of the use of isotopes in agricultural research, and Noggle (1951) has prepared a general outline of possible tracer applications to soil studies. Utilizing a new technique for the study of the behavior of plant root systems, Hunter and Kelley (1946) showed that radiophosphorus was absorbed by a guayule plant root, at a depth of 48 inches, from soil which was below the permanent wilting percentage.

In studies of phosphorus uptake by grape vines under field conditions, Ulrich, Jacobson and Overstreet (1947) showed that phosphorus supplied at the surface was not so efficient as that applied at some depth in the soil. The calculations based on radioactive measurements indicated that less than one per cent of the phosphorus added to the soil was contained in the aerial parts. Soil analyses showed that the surface-supplied phosphorus had penetrated only 11 inches in 43 days, while the water had penetrated at least 20 inches.

Three papers by Japanese workers—Okuda, Kasai and Anma—show the distribution of absorbed P^{32} in peanut and spinach (1951a), wheat (1951b) and sesame (1952). Early additions of marked phosphorus were found at harvest time to be accumulated in ears, leaves and stems, while later additions accumulated in roots.

TRANSLOCATION

The geographic tracing of specific radioactive elements constituted a major part of the early work with tracers, and since translocation in plants is still poorly understood, much more of this type of study will be required. Marker or tracer materials may include essential or non-essential mineral nutrients, metabolites marked with S^{35}, P^{32}, or C^{14}, etc., growth regulators marked with I^{131} or C^{14}, or water marked with tritium. In spite of the obvious con-

veniences of their use, the results obtained have not entirely meas-
ured up to reasonable expectations. The difficulty apparently
stems from the lack of suitable methods of introducing them into
the phloem. A solution of the problem would not only further
translocation problems directly but would also contribute to further-
ance of studies involving weed sprays, foliar application of ferti-
lizers, hormone control of physiological processes, etc.

Perhaps the first major conclusive contribution to this field, and
one which terminated a long period of uncertainty, was the clarifi-
cation by Stout and Hoagland (1939) that the radioactive isotopes
of potassium, sodium, phosphorus and bromine move upward
through the xylem tissue. It was shown, however, that if wood
and bark are in contact, the radioactive elements are rapidly
transferred laterally from wood to bark. Gustafson and Darken
(1937a, b) had previously made use of radiophosphorus to study
the upward movement of this element in the stems of several plants.
Their first conclusion was that radioactive phosphorus in the form
of phosphate is transported upward through the phloem system.
In a later experiment Gustafson (1939) reached the conclusion
that not so much mineral matter was conducted through the phloem
as he and Darken had previously supposed, but still maintained that
some upward conduction through the phloem is possible under
normal conditions.

Cyclotron produced radioactive sodium was used by Nisina and
Nakayama (1938) to show the rapidity of movement of Na in roots
and leaves of geranium, and in addition they cite experiments which
are reported to show that salt rises in both phloem and xylem
tissues.

Biddulph (1938, 1940) used radioactive phosphorus to show that
upward movement in the stem of bean plants took place rapidly and
followed the transpiration stream, with the greatest accumulation
taking place in the uppermost leaves. The downward movement
of this element in bean plants was then studied by means of a
technique wherein the radioactive tracer was injected into a veinlet
of a leaf in such a manner that back movement from the leaf took
place through the phloem. The method is not without limitations,
since it does open a vein and may under some conditions modify
the normal hydrostatic forces, particularly in the xylem. The di-
urnal migration from the leaf was followed (Biddulph, 1941) and

it was shown that much the greatest movement occurred during the daylight hours. The possibility of a relatively rapid " circulation " of phosphorus within the plant was shown. By means of a stripping technique similar to that of Stout and Hoagland (1939) which was previously mentioned, Biddulph and Markle (1944) demonstrated the downward movement of phosphorus in the cotton plant to take place through the phloem. The rate of movement was well in excess of 21 cm. per hour, and marked phosphorus was also found in the phloem sections above the point where the phosphorus entered the stem, thereby showing that a simultaneous upward movement could also take place in the whole phloem tissue.

Colwell (1942) studied the movement of phosphorus from leaves of squash plants and reached the conclusion that the movement of the radioactive indicator was restricted to the phloem and that the movement was correlated with food movement in the plant. Some additional information bearing on the movement of phosphorus in stems was obtained by Moore (1949) by the use of corn plants whose roots were divided in such a manner that each half of the root system was maintained in a different nutrient solution. Then by adding radioactive phosphorus to one solution he found that the marked phosphorus readily ascended the stem and after six hours some of it had descended into the opposite group of roots. Some labelled phosphorus could be detected in the solution bathing these roots after approximately 96 hours.

There is considerable advantage to be gained by the simultaneous use of two tracers in the same plant section. Rabideau and Burr (1945) made use of the stable carbon isotope C^{13} and radioactive phosphorus to study the simultaneous movement of carbohydrates and phosphorus. They found a rapid transport of labelled photosynthate both upward and downward in the stem to the metabolically active regions of root tip and stem tip. In its upward movement radioactive phosphorus passed through killed areas of bean stems, while compounds containing C^{13} did not. An additional contribution to this problem was made by Chen (1951). He obtained with willow cuttings substantially the same results as were obtained by Stout and Hoagland (1939). In addition, by supplying $C^{14}O_2$ to leaves of geranium plants at one level on the stem and P^{32} to leaves at a different level, he detected simultaneous but directionally opposite movement of C^{14}-labelled photosynthate and

P³² in the phloem. Since the stem had been previously stripped, the movement was shown to have taken place in the phloem tissue.

The factors which influence the release of mineral nutrients from roots into xylem tissue are not well understood, but some attempts have been made to determine the conditions which most favor this release. Broyer and Hoagland (1943) showed that large differences in transpiration had little influence on movement into the shoot, but they report that, under some conditions, reducing transpiration to the greatest possible extent may, for short periods at least, prevent movement of salts to the upward part of the shoot. They concluded that the role of transpiration in upward movement is not excluded despite the importance of metabolic factors. Broyer (1950) showed that in low salt plants, salts may migrate to vacuoles or to the xylem areas. In high salt plants migration along the symplast to the xylem takes place.

Hanson and Biddulph (1953) found a diurnal variation in the amount of rubidium and phosphate which was translocated to the shoot in bean plants. The maximum occurred near midday and the minimum near midnight. Superimposed on the diurnal pattern are effects due to the metabolic status of the roots. Those roots which absorb the most ion, by reason of adequate supply of metabolite or a low salt–high sugar nutritional status, will also translocate a greater percentage of the ion to the shoot. Xylary translocation of radiophosphorus in pine has been correlated with anatomical structure to explain an observed difference in the rate of movement within stems and roots (Moreland, 1950).

As previously mentioned, Hevesy, Linderstrom-Lang and Olsen (1936, 1937) employed an isotope dilution technique which demonstrated the rapid interchange of phosphorus atoms between parts of both corn and sunflower plants. A similar experiment using N¹⁵ showed rapid interchange of N¹⁵ into proteins as well as rapid geographic interchange between leaves (Hevesy et al., 1940). Using wheat seedlings with parted roots, one part being placed in an inactive solution and the other in a radioactive phosphorus-containing solution, Hevesy (1947b) showed a migration through the plant from the active to the inactive solution.

That translocation studies have progressed to the stage where it is possible to discuss circulatory disorders in plants is the object of a report by Biddulph (1951). Particular attention is given to

the effects of phosphorus and other factors on the mobility of radio-iron in bean plants. Rediske and Biddulph (1953) have pointed out that iron is almost completely immobilized in bean plants grown at medium to high phosphorus levels, and a pH of 7.0 or above. Iron is readily phloem mobile only if the plants are low in phosphorus and iron, and are growing in an acid medium near pH 4.0. Some additional information on the mobility of phosphorus, sulfur, calcium and zinc is reported in a later publication (Biddulph, 1953). Phosphorus and sulfur were shown to be particularly mobile in the phloem, iron and zinc conditionally mobile and calcium practically immobile.

METABOLISM

CALCIUM. The radioactive isotopes of calcium and their suitability as indicators in biological systems were described by Walke, Thompson and Holt (1940). They describe the isolation of the various calcium isotopes, including Ca^{45}, from bombarded materials. Since that time little use has been made of this element in plant studies. Bledsoe, Comar and Harris (1949) used Ca^{45} to study the uptake of calcium by peanut fruit. They showed a very limited movement of root-absorbed calcium into the developing fruit, but when tracer calcium was placed in the environment of the young pegs, the developing fruits readily absorbed it. The failure of root-absorbed calcium to move into the fruits indicated a lack of mobility of calcium in the phloem, which is in keeping with the general opinion that calcium is not readily phloem mobile. The developing peanut fruit is then dependent upon direct absorption of calcium and does not utilize that which is absorbed by the root. Biddulph (1953) has also demonstrated that calcium is almost completely immobile in the phloem of the bean plant.

Procedures for the use of Ca^{45} in plant and animal studies have been presented by Comar et al. (1951). Calcium has not been extensively used as a tracer in plant studies. It offers a number of advantages which would warrant much more extensive use: it has a long half-life, i.e., 180 days, and can be obtained in sufficiently high specific activity for most biological studies.

COPPER. Mazia and Mullins (1941) immersed *Elodea* leaves in very dilute solutions of radioactive copper chloride (Cu^{86}) and found that the cells were able to accumulate copper in excess of

3×10^8 of that present in the nutrient media. They conclude that the effects of copper are due to the power of protoplasm to bind these ions against a concentration gradient rendering them available for the physiological processes in which they participate.

IODINE. Many uses have been made of radioactive iodine in animal studies, and it has been employed in connection with other radioisotopes in several plant studies; but the only attempt to study the metabolism of radioactive iodine in plants was made by Kelly and Baily (1951) for brown algae. By the use of the tracer it was shown that a steady state of iodine content is reached, after which further increase does not occur. There is a continual exchange between the iodine within the plant segment and the iodine in the surrounding medium.

IRON. Manganese interference in the absorption and translocation of radioactive iron (Fe^{59}) in pineapple has been reported by Sideris (1950). Most iron which was removed from the nutrient solution was deposited in the roots, especially in the cultures containing manganese. The amounts of iron translocated from the root to the leaves was correspondingly lower in the plants grown in the presence of manganese. Considerable amounts of the translocated iron remained in the proteinaceous matter of the cell.

Rediske and Bidulph (1953) studied the absorption and translocation of radioactive iron (Fe^{55}) in bean plants. The factors which influenced the distribution of iron in a plant were discussed, and it was shown that iron could be readily immobilized within the tissue or that it could remain free for translocation. The factors which tended toward immobility were high phosphorus content of the tissue and growth in a nutrient media at pH 7 or above. Iron remained freely mobile in those plants wherein the iron and phosphorus content of the tissue was low and their roots were immersed in an acid nutrient medium of approximately pH 4. Autoradiographs of chlorotic and green leaves show the different distribution patterns of iron in these instances.

MANGANESE. Millikan (1951) has presented a rather comprehensive picture of the behavior of radioactive manganese (Mn^{54}) in flax, peas, cabbage and tomato plants. A number of cases of irregular distribution of manganese in senescent tissues are described as well as the distribution in normal healthy tissue. Suc-

cessive autoradiographs of the same pea plant showed that manganese moves from the interveinal tissue into the veins as the plant dries out. This indicates that some caution is required in preparing plant parts for autoradiographs if the drying procedure is followed.

MOLYBDENUM. Stout and Meagher (1948) present a complete accounting of the absorption and subsequent distribution of a single microgram of molybdenum in a growing plant. They show that it is readily absorbed and translocated, as are other microelements such as manganese and zinc. They present autoradiographs showing the comparative distribution of K^{43}, Mo^{98} and Mo^{99}, and conclude that molybdenum shows a different type of distribution within plant tissue than do the other mineral nutrients, potassium, phosphorus, manganese and zinc. Phosphorus was reported to have a distinct influence on the absorption of molybdenum.

PHOSPHORUS. The first use of radioactive phosphorus in plant studies was reported by Hevesy, Linderstrom-Lange and Olsen (1936, 1937). They employed an isotope dilution technique in order to show the exchange of phosphorus atoms between older and younger leaves of corn and sunflower, respectively. This marked the beginnings of the use of this element in the tracing of metabolic paths in plants. The early work with this element was largely from cyclotron-produced phosphorus 32. The cyclotron-produced radiophosphorus persisted as the sole practical source of this element until after the diversion of some of the pile facilities for the manufacture of this and other radioactive elements at the termination of the recent war. The quantities which were available were limited, as compared to present supply, but served admirably for certain types of studies involving migration and deposition.

Brewer and Bramley (1940) and Brewer (1941) used radioactive phosphorus and sodium to show the rapidity of appearance of these elements in leaves after their administration to the roots. They also showed some back diffusion of sodium from the plant to the nutrient medium. Only a very slow back diffusion of phosphorus occurred. Arnon, Stout and Sipos (1940) made a more extensive study of the distribution of phosphorus in tomato. Phosphorus was shown to move from the solution to the tops of six-foot tomato plants within 40 minutes. The greatest capacity for phos-

phorus uptake was shown by young fruits, although the element moved readily to all parts of the plant.

In a study of the effect of the form of available nitrogen on the absorption and distribution of phosphorus by the tomato plant, Breon et al. (1944) showed that plants furnished urea absorbed P^{32} at a much more rapid rate than those furnished with nitrate. Also those plants lowest in phosphorus absorbed P^{32} the fastest. The distribution of the absorbed P^{32} in the ether soluble, alcohol soluble, water-acid soluble, and the insoluble fraction is given. Phosphorus compounds synthesized by the plants were in about the same proportion for the phosphorus deficient and normal phosphorus plants, but the rate of synthesis was faster in phosphorus deficient plants. Biddulph and Brown (1945) followed the movement of phosphorus into developing cotton flowers and attempted to correlate the movement of phosphorus into the developing flowers and fruits with the morphological events of synapse and fertilization. It was shown that the highest concentration of phosphorus was in young primordia and decreased progressively thereafter. Small gains were made with each morphological event, but on the basis of per cent the phosphorus continued to decrease with maturation of fruits. Withner (1949) presents a dynamic picture of phosphorus movement into various parts of corn plants during the course of their development.

Some of the factors which influence the uptake of phosphorus by bean plants were studied by Biddulph and Woodbridge (1952). The distribution of phosphorus in this plant as influenced by pH and phosphorus concentration was reported. The presence of iron in the nutrient media had some influence over the amount of phosphorus available for metabolic use when the supply of this element was extremely limited. The distribution of phosphorus in soybeans was shown by Klechkovskii et al. (1947). Their study compared the distribution which was obtained by plants having adequate phosphorus nutrition with plants on a sharply curtailed supply.

√ An interesting application of radiophosphorus has been made by Sisakyan and Voronkova (1950) and by Klechkovskii, Stoletor and Evdokimova (1951) in an attempt to study the compatibility between the stock and scion of grafted plants. This idea might easily be extended to a study of the mechanism of dwarfing of certain stocks; of resistance to chlorosis, virus diseases, etc.

Studies of phosphorus absorption and distribution in inbred and hybrid maize have been reported by Rabideau et al. (1948, 1950). It is interesting to note that a tracer can be used to show differences in phosphorus metabolism by these genetically different plants. Tsao, Rabideau and Whaley (1950a) have also studied the phosphorus uptake of *Andropogon* species at various stages of development, and the effect of phosphorus nutrition on nitrogen absorption of four species of grass (1950b).

The absorption of radioactive phosphorus by mycorrhizal roots of pine was studied by Kramer and Wilbur (1949). They showed that mycorrhizal portions of pine roots accumulated much larger quantities of phosphorus than non-mycorrhizal portions. Kramer (1951) later studied the effects of respiration inhibitors on the accumulation of P^{32} by mycorrhizal and non-mycorrhizal roots of pine and reached the conclusion that, in general, pine roots seem to react to respiration inhibitors in about the same manner as barley and tomato roots. The non-mycorrhizal roots appeared more sensitive to azid and fluoride inhibitors than mycorrhizal roots. Tsao and Whaley (1950) report that plant gall tissue accumulates more phosphorus than healthy adjacent tissue and suggest that metabolic differences may be responsible for the accumulation.

A very interesting application of phosphorus-containing fertilizers as foliar amendments has been made by Silberstein and Wittwer (1951), who have shown that foliar applied phosphorus was utilized much more effectively than phosphorus applied broadcast to the soil, even though the latter treatment gave highest total yields. A concentration of 25 to 50 millimoles of phosphorus per liter was found most desirable for the greatest movement of the compounds which were tried. Generally, o-phosphoric acid was the most effective of all chemicals tried. The foliar phosphorus was traced to all parts of the plant, including root tips, and to the areas of high metabolic activity. Apparently within 48 hours after treating, five to six per cent of the total phosphorus in developing tomato fruit may be derived from a single foliar application of o-phosphoric acid. Eggert, Kardos and Smith (1952) applied tracer phosphorus to apple trees, both as foliar sprays and as soil amendments. A single foliar application resulted in uptake amounting to two to three per cent of the total P_2O_5 of the trees. There was continual absorption for 30 days after application, even though

no subsequent rain or water spray was used to moisten the leaves. About half of the leaf-absorbed phosphorus was translocated to the root; the cores, seeds and subepidermal tissues of the fruit were the highest of the aerial tissues. No uptake of soil-applied tracer phosphorus could be detected under any of the regimes tried. The tracer phosphorus was more efficiently absorbed from diammonium phosphate than from several other phosphorus-containing compounds. The mobility of phosphorus within bean and cotton plants was shown earlier (Biddulph, 1941; Biddulph and Markle, 1944) and this type of application is a natural development for elements which are readily phloem mobile (Biddulph, 1953).

SULFUR. The first use of radioactive sulfur in plant studies was by Thomas et al. (1944). These authors used sulfur in the form of sulfur dioxide in order to show the uptake of it through the aerial portions of the plant. They found a high initial absorption of sulfur dioxide by the leaves, followed by a lowering of the concentration as the sulfur was distributed throughout the plant. Translocation was assumed to be in the form of sulfate. Root absorption studies, using a single application of radioactive sulfur as sodium sulfate, showed that the concentration of the leaves built up to a maximum in eight to ten days. This was followed by a lowering of the concentration as sulfur was redistributed. They found that top concentrations were higher than root concentrations for both wheat and barley. Distribution of sulfur was also studied in corn; the highest concentration was in the leaves with the least in the stalks and husks. Because of the stage of maturity, distribution in the developing ear was not studied. The radioactive sulfur was traced into the various fractions—sulfate, acid soluble, acid insoluble and labile sulfur.

In connection with this work, Harrison, Thomas and Hill (1944) used an autoradiographic procedure which was able to show the distribution of sulfur in the developing tissues of wheat. Rather uniform distribution of sulfur in wheat leaves was reported, but the highest concentrations were found in the kernel which was sampled at the dough stage. There was a particularly marked concentration of sulfur in the embryo and in the periphery of the endosperm, especially the aleurone layer. The distribution through the tissues appeared to be similar, whether the sulfur entered as sulfur dioxide or as sodium sulfate.

The sulfur metabolism of alfalfa was also studied (Thomas et al., 1950). Their experiment showed that in sulfur-deficient plants a maximum concentration in the leaves was reached in 16 days. Sulfate was gradually converted into the organic form. When the plants were cut back and the new shoots exposed to sulfur dioxide there was a very rapid uptake of radiosulfur with a corresponding rapid conversion into the organic form. The sulfate in the roots was not changed into organic forms unless top growth was present.

A translocation experiment was conducted by dividing the shoots and dipping the tops of one group into a solution of radiosulfate. The absorbed sulfate was translocated down the stem where it was changed steadily into the organic form. Some sulfur passed down through the crowns or roots and reappeared in the leaves of the undipped stems where it was also changed into the organic form.

Fried (1948) studied the absorption of sulfur dioxide by the aerial parts of alfalfa plants. He sealed the soil surface in order to isolate the roots and tops from each other in an attempt to exclude the possibility of root absorption of sulfur dioxide. He confirmed the finding that alfalfa plants can take in sulfur dioxide through the leaves and convert it into organic sulfur compounds. Autoradiographs were used to show the distribution of sulfur in the plant parts.

The amount of absorbed sulfur necessary for destroying rust and mildew infections without injury to the host was determined by Yarwood and Jacobson (1950), using sulfur 35. One to three μgm. of sulfur per square centimeter of leaf area was required while the leaf could stand from three to six μgm. with only slight injury. They concluded that selective absorption by diseased tissue (host and pathogen) may explain the chemotherapeutic effect.

Sulfur has been used frequently as a fumigant for various fruits, and it has been shown by use of S^{35} that sulfur vapor penetrates into citrus fruits and is incorporated into various sulfur-containing compounds (Turrell and Chervenak, 1949). In a rather exhaustive study Turrell (1950) has shown that various environmental factors may influence the relative distribution of the radioactive sulfur used as a fumigant in the sulfur compounds of the fruit.

SODIUM. Data on radioactive sodium (Na^{22}) uptake per cm.^{2} of leaf area as a function of the sodium concentration in the nutrient medium is given for corn by Brewer (1941), and the inter-

relationship of sodium and potassium in plant nutrient studies was shown by Leonard and Toth (1950) by the use of Na^{22}. The radioactive sodium tended to concentrate in the conducting tissues of the plants. The salient features of the Na^{22} distribution in several species of plants were described. Both activity measurements and autoradiographs were used to portray the distribution.

ZINC. A study of the metabolism of Zn^{65} in peas by Bergh (1951) shows that the root had the highest zinc content and the older leaf blades the lowest. Seventy-seven per cent of the zinc associated with the root remained insoluble, whereas in the aerial portions—shell, leaf blades and stems—65 to 85% of the zinc was soluble in cold water. The insoluble residue appeared to be fixed in the proteins. See also Stout et al. (1947) for a study of the zinc metabolism of tomato.

RADIATION INJURY

In this discussion no attempt is made to survey properly or review the effects of radiation on plants. However, insofar as the radiation emitted by " tracers " may influence the physiological process studied, it seems desirable to include that literature which establishes or attempts to establish a safe level of radiation for tracer studies. It is important not to employ a tracer yielding sufficiently intense radiation to disrupt or alter the process under consideration.

Radiation from the natural radioactive materials has long captivated the imagination, and it appears to have been difficult, at least for the uninitiated, to refrain from assigning magical powers to it—either for good or for evil. In the early literature, Gager (1907) became interested in atomic disintegrations (radioactive) vs. molecular disintegrations (destructive metabolism) and the crude analogies between them. While it was claimed that radioactivity is in no sense comparable to metabolism, it was considered desirable to establish the fact that radioactive substances are incapable of independently elevating inorganic compounds to the state of those found in living organisms. There are a number of reports extending to relatively recent times (Leggieri, 1940), claiming that physical effects from radioactive waters were apparent. Brief immersion of vetch beans and corn in radioactive water was claimed to have a stimulative effect, but prolonged immersion was unfavorable.

The list of physiological processes which were influenced was rather long. It has been very difficult to confirm or deny that radiation from relatively weak sources has stimulative properties. The difficulties encountered are not only inaccurate measurement of the radiation but also quantitative appraisal of plant behavior.

The influence of naturally occurring radioactive elements on growth and yield of plants has been reported by Drobkov (1937, 1939, 1940). Increases in yield of peas up to 182% in the first and as high as 204% in a second report are claimed. Even nitrogen fixation by legumes is reported (1945) to have been influenced. French (1948), as the result of experiments on five vegetables, concludes that the use of radioactive materials in conjunction with commercial fertilizers tends to increase the mean yield of many crops.

Perhaps the most comprehensive survey of the effect of radioactive materials on yields of plants has been made by Alexander (1950) who attempted on a sound and systematic basis to appraise the effect of radioactive stimulants on the yield of plants in the field. Alpha rays from actinium in " alphatron " together with radium and uranyl nitrate were the three sources of radiation. After careful experimentation, the general conclusion to be drawn from the data was that no effect of the radioactive materials was found either beneficial or harmful. There were a few cases where differences reached the five per cent level of significance, but they were no more than would be expected in sampling from normal distribution.

Until further carefully conceived experiments are designed which yield evidence to the contrary, the writer feels it justifiable to conclude that stimulatory effects resulting from radiation have not been established.

Simultaneously with the use of radioactive tracers it became desirable to attempt an establishment of the level at which radiation damage first occurred. Since radiation effects on living tissue are extremely complex, a satisfactory quantitative test for injury was not immediately apparent. It became necessary as each physiological process was studied to determine the effects of radioactivity from the tracers on that particular process. As a result, there is accumulating in the literature considerable quantitative data on the effect of ionizing radiation on living tissue.

Brooks (1939) showed that there is no observable effect on oxygen consumption, as indicated by the Warburg method when *Nitella* was exposed to the radioactivity of sodium between the limits of 2.2–12 mc./l. Mullins (1939*a*) showed that radiation from radioactive sodium decreased the amount of penetration of sodium ions into *Nitella* cells when the concentration of the radioactive ion exceeded one mc./l. The decrease was principally of " induced accumulation " due to a decrease in the number of exchange positions of the protoplasm. Radioactive K^{42} could also be shown to produce the same effect (Mullins, 1939*a*). Muir (1942) showed that beta radiation from radioactive phosphorus increased the viscosity of the protoplasm of *Spirogyra* when the strength of the radioactive solution was four to 17 mc./l. but had no effect when the radioactive strength was 2.1 mc./l. Some changes noted in total phosphorus may have resulted from effects upon permeability of beta radiation from the radioactive isotopes.

Weintraub (1944), in a review of radiation and plant respiration, concludes that under some conditions an increase in the rate of " apparent " respiration, as measured by gaseous exchange, may be induced by radiation of various species of plants and types of tissue. He was unable to decide whether the observed stimulation was directly related to " true " respiration. He concludes with the statement that, " Despite the long continued interest in this problem, the results available are almost entirely of a descriptive nature and in no single case has there been presented, as yet, a satisfactory illucidation of the mechanisms involved ".

Spinks et al. (1948) used P^{32} and Sr^{90} as radioactive sources and observed a lethal limit of absorbed radioactive isotope between 0.0065 Rd per seed and 0.065 Rd per seed for wheat, barley and sunflower in the seedling state. Sunflower proved somewhat more resistant than wheat and barley. Dion et al. (1949) used radioactive fertilizer phosphorus at 26 mc. and 260 mc. per gram of phosphorus and concluded that there were neither harmful nor beneficial effects observable at this rate of application. Russell and Martin (1949) used P^{32} at activities between 0.5 and 50 $\mu c./l$. As a result of these investigations they concluded that radiation damage may be a much more serious hazard than previous literature had led them to believe. They found significant radiation effects when the level of P^{32} is ten $\mu c./l$. These authors worked with rapidly

growing young plants where phosphorus accumulation was high. Blume et al. (1950) used barley grown in nutrient culture exposed to P^{32}. They concluded that damage to tops was more severe than damage to roots and that injury was due to the radiation from P^{32} accumulated in the plant; the P^{32} remaining in solution had relatively little effect. Damage to cells was manifested in the zones of active cell division, and the lowest level at which damage was discernible corresponded to 5.6 mc./gm. of P_2O_5.

Bould, Nicholas and Thomas (1951) concluded that radiation effects on the growth and physiology of barley and tomato do occur at low radioactive dosages, lower than those accepted as " safe " by some investigators. They state that the most striking feature of their experiments was the smallness of the radiation effect despite the fact that they worked at concentrations of P^{32} in excess of those which would normally be used in tracer work. They were not concerned with morphological or cytological abnormalities which may have occurred in tissue, but considered only the criteria which would be used in plant nutrition studies in soils.

Some effects of high concentrations of P^{32} on the growth of potato have been reported by Stanton and Sinclair (1951). Dosages of the order of 3,000 r received by the growing points in the first fortnight were responsible for rather striking abnormalities. The abnormalities included increased fleshiness of leaves, loss of secondary leaflets, increased branching and the appearance of what is termed " blind " plants, in which the main shoot terminates in three leaves surrounding an aborted growing point.

Because of the interest in the possible spread of fission products as a result of atomic weapons and disposal problems associated with the manufacture of plutonium, it becomes desirable to investigate the effects of fission products on plants. Jacobson and Overstreet (1948) have made a study of uptake of fission products and plutonium adsorbed in soil colloids. They found that barley and pea plants were able to take up fission elements Y, Ce, Zr, Cb, Sr and the three valence states of Pu, even when these elements were present in trace amounts on the surfaces of clay or soil particles. The greatest fixation is in or on the roots, and with the exception of Sr, translocation occurs only to a limited extent. The translocation of Sr is relatively large, i.e., 0.1 μc./gm. of soil acting over three months supplied sufficient strontium to the tops to show

" radiation injury ".   Within the soil, activity levels of 0.1 μc./gm. of soil were sufficient to cause very pronounced injury over a three months' period.

Mackie et al. (1952) have shown that " plants grown in solutions of comparatively low specific activity exhibited clear evidence of damage to shoot meristems, but no apparent injury to root tips. Measurements . . . gave no indication of a threshold value for radiation effect upon meristematic cells ".   " By extrapolation . . . one might expect that some injury to the plant would occur from the application of any amount of ionizing radiation, regardless of how small.   It does not follow that this injury, when slight, would be reflected in more permanent symptoms of abnormality ".

There is a very lively interest in the biological effects of radiation at the present time.   This subject is far too extensive to be reviewed here.   My desire is merely to point up the need for careful consideration in choosing levels of radioactivity which will not invalidate the results expected from a particular experimental design.

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THE BOTANICAL REVIEW

THE PHYTOGEOGRAPHY OF UNGLACIATED
EASTERN UNITED STATES AND
ITS INTERPRETATION

E. LUCY BRAUN [2]

INTRODUCTION

Unglaciated eastern United States is here interpreted as in-
cluding the area south of the limits of continental ice sheets and
east of the 98th meridian, i.e., the forest area in contrast to the
grassland. The Driftless Area of southwestern Wisconsin and
adjacent Illinois, Iowa and Minnesota, and the small unglaciated
spots in eastern Canada are not included, except as their features
may help to explain problems in the area under consideration.

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[1] The spellings " Southern Appalachians " and " southern Appalachians "
have been retained in this article in order to emphasize specificity in the case
of the former; and the forms " peneplain " and " peneplane ", " relic " and
" relict " have been retained in deference to the authors cited.
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The literature of floristic plant geography for the most part deals with isolated species or groups of species, or with the features of limited areas differing vegetationally and floristically from the prevailing types. The unusual, rather than the usual, has attracted attention, and often proves of great value in reconstructing past events. The only more or less comprehensive treatment is included in Harshberger's " Phytogeographic Survey of North America " (112). Here, in addition to depicting regional vegetation through descriptions (with floristic lists) of specific local areas, Harshberger includes theoretic considerations dealing with the geologic evolution of floras, the history of floras and the affinities displayed. His map (p. 206), illustrating centers of plant dispersal determined by glaciation, long remained the embodiment of current ideas. More recent investigations have changed the details, although some of the basic ideas remain. Many of the floristic districts which he located and characterized are still recognized. His statements concerning affinities of North American floras do not depart greatly from present-day beliefs, although some of his examples cannot now be used, and some of his geologic interpretations must be revised.

Two principal divisions of unglaciated eastern United States may be recognized: (a) an older upland area which includes the Appalachian Highlands and Interior Low Plateau to the east of the Mississippi River, and the Interior Highlands (Ozark and Ouachita provinces) to the west of the Mississippi River; (b) the younger coastal plain area. The dominant vegetation of the older area is deciduous forest, made up largely of species belonging to genera of wide distribution in temperate latitudes; coniferous communities are more or less local. In the younger area, deciduous forest communities and their associated species are more circumscribed, while evergreen species, both needle-leaf and broad-leaf, assume prominence, and a tropical or subtropical element is conspicuous in the flora. In both of these areas, local communities, apparently not in accord with the regional vegetation, occur. Disjunct occurrence of species is frequent—of upland species in the coastal plain area, of coastal plain species in the upland. Such extraneous species often give clues to past events. Endemics, some local, some approaching " wides " in the extent of their ranges, are numerous on the Coastal Plain and in

the Appalachian Highlands, less numerous but present in the Interior Low Plateau and the Interior Highlands.

The existing pattern of distribution is a result of present and past conditions of the environment. Edaphic factors play an important role in determining local distribution. Topographic factors, through their influence on soils and soil moisture, and on local atmospheric factors, are also important. They determine, in large part, the microclimates of an area, in contrast to the regional climate. But topography changes, and consequently, through geologic time, the physiography of large areas gradually changes in accord with the progress of the erosion cycle. One type of habitat will decrease in extent, while another increases. Species ranges must shift with such environmental changes, or ecotypes develop which are suited to certain microclimates of the changed area. Climate determines potential range, within the limits set by local factors. But climates have changed in the past, and therefore the ranges of species or whole groups of species—communities—change; enforced migrations take place. Migration often results in disjunction of range; in isolation of relatively small units of the population of a species; in gradual change in morphologic characters of a species from one part to another of its changing range; in contacts between related species formerly entirely distinct in range but capable of hybridizing when they come in contact.

Disjunction—brought about by advancing migration—may result when dispersal and changing conditions permit establishment in a new location. It may result, also, when changing conditions allow influx of new and different populations which crowd out the former occupants or surround them where they remain in isolated colonies. Disjunction of the latter kind is more frequent. Such disjunction of range may be brought about when previously continuous habitats—edaphic, topographic, or climatic—are disrupted by topographic processes or by change in continental configuration or climate. Persistence of disjuncts depends on fitness of the local environment, and often, in addition, on lessened competition due to the unsuitable character of the local environment for the regional vegetation type. The compensating effects of the local environment may overcome the unfavorable character of the regional environment.

Isolation, brought about by disjunction, may result in the evolution of distinct varieties or even species. Ordinarily, this is evident only after a long period of separation, but in some instances, changes are rapid.

Because most species are variable and composed of a number of biotypes having slightly different tolerances, changing conditions and migration may result in partial segregation of variants which are arranged along a gradient from one extreme to another. Or, changing conditions may result in the destruction of biotypes and ecotypes, resulting in reduction of range of formerly widespread species. Further depletion of biotypes may result because of isolation of small populations (183). On the other hand, hybridization is made possible either by the break-down of ecologic barriers (usually by modified conditions) or by contacts brought about by shifting populations and reduction of extent of barriers during climatic and physiographic changes. Thus came about the hybridization of species of *Iris* in the Mississippi delta (8, 202) and in the interior where ranges were modified by glaciation (7); in *Tradescantia* (7, 8); in *Vaccinium* (43); in fact, in many genera. Repeated back-crossing sometimes tends to obscure the hybrid nature of resulting forms; it results in the " gradual infiltration of the germplasm of one species into that of another "—introgressive hybridization. As Anderson (9) points out, " all the widespread eastern species which have so far been analysed exhibit introgression along the Ozark-Texas axis, if they have a related taxon in that direction ".

The interpretation of existing phytogeography must be based on evidence gleaned from a number of unlike sources: from the distribution pattern itself, the relationship of species and communities, their geographic extent or degree of continuity or disjunction; from the correlation between distribution and physiographic and climatic history; from the physical features of the environment, which alone or in part may explain existing distribution; from hybrids and population variation; and from fossils. Obviously, this leads us into a number of diverse fields—floristics, involving modern taxonomy and genetics, synecology, pedology (including permafrost features), climatology, physiography and paleontology.

Much of the information of significance for phytogeographic

studies is hidden in a mass of irrelevant material. Statements here and there, often without correlation with distribution, will add to the sum total of knowledge bearing on past migrations and present distribution. A search for all of these in the literature of the diverse fields of science relevant to our topic is not possible; yet some references of this sort will be given in order to emphasize the expanding future of phytogeographic studies. A number of publications treat plant geography in its broad aspects, or emphasize the underlying principles and related topics; chief among these are books by Cain (38), Good (96) and Wulff (218).

FLORISTICS

Interest in the floristics of eastern North America was first aroused by Asa Gray, who more than a century ago (97) pointed out the remarkable resemblance between the floras of eastern America and eastern Asia, and offered the then remarkable suggestion that " the extant vegetable kingdom has a long and eventful history, and that the explanation of apparent anomalies in the geographic distribution of species may be found in the various and prolonged climatic or other physical vicissitudes to which they have been subject in earlier times;—that the occurrence of certain species, formerly supposed to be peculiar to North America, in a remote or antipodal region affords of itself no presumption that they originated there ". In a series of later papers (162) Gray continued to make comparison between American and other floras, and to point out special features of our flora. Decades later the problem of relationships of floras, of specific segregations and identities, gained renewed prominence because of Fernald's publications (83, 84).

In plant geography it has been more or less customary to refer to the " elements " of a flora, and to " floristic affinities " and relationships. " Element " has been used in a variety of ways, frequently in combination with a defining adjective, as northern element, Appalachian element, Tertiary element, endemic element, relic element, etc. Although attempts have been made to confine its use to the geographic sense, the more acceptable usage is a broad one (38, 218). Affinities refer to the elements displayed by and relationships of the flora of a natural area; and sometimes, more artificially, to the flora of a political unit, as a state.

Throughout the East the Tertiary element is prominent. This is the so-called Arcto-Tertiary flora.

A considerable number of genera of the Arcto-Tertiary flora are circumboreal in distribution; others are restricted to eastern America and eastern Asia; a few are confined to one continent. They are generally conceded to be restricted remnants of the widespread mesophytic mid-Tertiary floras whose genera date from Cretaceous or early Tertiary time. Evolution through the millions of years following separation, restriction of range and ultimate isolation has indeed been slow, for differences between the species of genera of eastern American-eastern Asian or eastern American-European distribution are sometimes slight.

The term " Arcto-Tertiary " was introduced as " Arctic-Tertiary " by Engler to designate the flora of the Arctic in Tertiary time, a flora similar to that of our temperate latitudes today. However, as Wulff (218) points out, this was not an arctic flora, and the term may therefore be misleading. It was a temperate flora, and the warmer-climate Tertiary flora of slightly lower latitudes (called " boreal-Tertiary " by Engler) was a warm-temperate or subtropical flora. Li (123) suggests that the term " Tertiaro-mesophytic " be used for this element of our flora. However, there seems to be little reason to displace the established term. Arcto-Tertiary may be defined as the flora which " had its wide development at high northern latitudes " and which " lived in a region of summer rainfall and winter cold, as judged by the habits of related living trees " (52). The Arcto-Tertiary flora " may be subdivided into typically temperate and boreal units " (50).

Some of the eastern American species of the typically temperate Arcto-Tertiary flora belong to genera of circumboreal range (e.g., *Salix, Quercus, Betula*); some are circumscribed in range (most of our so-called Tertiary or Miocene relics); and some belong to genera of eastern American–eastern Asian distribution but are widely distributed in eastern America. Genera with examples of widely distributed American species are *Liriodendron,* with one closely related species of restricted range in Asia; *Sassafras,* with two Asiatic species of somewhat limited range; *Magnolia,* with wides in both hemispheres; *Epigaea,* whose one Asiatic species is rather limited in range; and *Stylophorum,* with medium ranges in

both America and Asia. Ranges of the American species of the last two examples, as well as of many other species, are in part determined by edaphic factors; *Stylophorum* is generally confined to rich woods on calcareous soils; *Epigaea* to a somewhat drier type of woods on non-calcareous soils. In these cases geographic distribution of calcareous rock influences the range of species, both of which illustrate the American-Asian disjunction, and both of which must have had comparable geologic history. Both of these, also, may be used as examples to illustrate the importance of environmental factors in limiting present species ranges, of " historical factors " in accounting for presence and persistence to the present time, when local environment becomes operative in determining precise range. Mason (126, 127) would place more emphasis on the local environmental factors of the present, and objects to the phrase " historical factor ", although he does concede that " the history of a plant species may tell the very important story of *how* it arrived in any given place and *where* it came from ".

EXTRA-CONTINENTAL RELATIONSHIPS

The eastern American–eastern Asian and American-European or American-Eurasian relationships are most pronounced in the floras of the upland (older) areas of eastern United States; the tropical affinities, in the flora of the Coastal Plain. The latter, on the whole, are more remote. A North American–South American relationship is evident in a few plant families; this is well illustrated by the huckleberries (42).

The American-Asian and American-European relationships involve many instances of close specific relationship and even of specific identity. A considerable number of common genera have representatives in America, Europe and Asia (as *Fagus, Acer, Castanea, Populus*), species for the most part of the holarctic flora. Some are confined to America (sometimes both east and west) and southeast Europe and/or nearby southwestern Asia (as *Platanus, Cercis*), or are in these two places and eastern Asia (as *Liquidambar*). Other genera are restricted to eastern America and eastern Asia. Some of these (as *Carya*) are better represented in America; others (as *Magnolia* and *Astilbe*) in Asia; still others have only two or three species in the two areas

(as *Liriodendron, Sassafras, Stylophorum, Shortia*). Most of the species originally thought of as identical are no longer so considered; some, instead, are thought of as closely related pairs of species, or in a few instances as varieties of a single species. Almost 25 years ago Fernald (84) pointed out " that in nearly all groups the species of the Western Hemisphere are completely segregated from those of the eastern; that we have stable or essentially stable specific entities ". As examples of pairs of closely related species are *Liriodendron tulipifera* of eastern America and *L. chinense* of central China, limited in distribution and not discovered until 1873 (123); *Gymnocladus dioica* of America and *G. chinensis* of central China. As examples of the varietal relationship may be cited *Circaea quadrisulcata* of Asia and its variety *canadensis* of eastern America; *Ranunculus gmelini* and its two American varieties; *Polygonum sagittatum* of eastern America and its Asiatic varieties (101, 102). As may be expected, there are sometimes differences of opinion as to the status of taxa, as to whether certain taxa are specifically distinct or are only varieties of a single species—for example, *Tovara virginiana* (86, 123, 176) and *Mitchella repens,* whose Asiatic representative is sometimes considered only a variety (123). In some cases the resemblance between the American and Asiatic species is superficial, and the relationship is generic only. On the other hand, no varietal differences can be discerned in *Symplocarpus foetidus, Caltha palustris* and *Monotropa uniflora.*

The change in viewpoint concerning specific identity in no way lessens the importance of the real problem, one of startling relationship between remote areas.

The greatest concentration of plants of restricted range which display the eastern American–eastern Asian affinity is in the southern part of the Appalachian Highlands, particularly in the southern section of the Blue Ridge province, including the Great Smoky Mountains, the Blue Ridge and the many shorter more or less transverse ranges of the area. Here, too, are endemic representatives of genera of wider distribution, but genera whose maximum development is in the Southern Appalachians and mountains of Asia, e.g., *Rhododendron.*

Probably most of the better known examples of plants with Old World relatives are those mentioned by Fernald, as the American

species of *Shortia, Buckleya, Diphylleia, Stewartia* and *Neviusia* among the local endemics, and of *Liriodendron, Cladrastis, Hamamelis, Sassafras* and many others among the endemics of wider range (83, 84).   He points out that " In the ancient Appalachian Upland of the United States the outstanding phytogeographic feature is . . . the great mesophytic forest of Mesozoic or early Cenozoic genera, many of them formerly found likewise in Europe, western America and the Arctic but now restricted to one or more areas of eastern North America, eastern, central or southwestern Asia or the geologically ancient peninsulas of southeastern Europe ".

Of all the local endemics, *Shortia galacifolia* has received most attention because of its interesting history of discovery and rediscovery.   First found by André Michaux in 1788, it was not—in spite of Asa Gray's diligent search—rediscovered until 1879. Since then it has been located in a number of places in the mountainous area where North Carolina, South Carolina and Georgia come together, i.e., in the headwaters of the Keowee River and in the tributaries of the Catawba River about 70 miles to the northeast (38, 65, 72, 115, 116).   It grows on steep banks in the shelter of *Rhododendron, Kalmia, Magnolia,* hemlock and white pine, where such ground-cover evergreens as *Asarum virginicum, Galax aphylla* and *Mitchella repens* occur.   All three species of *Shortia* (*S. galacifolia* and the two Asiatic species) are very local mountain plants.   All are considered Tertiary relics representing restricted remnants of a former wide distribution of ancestral forms. That former wide range [3] was modified, disrupted and curtailed by events of Tertiary time.   As all known stations are within 15 miles of the divide between Atlantic and Gulf drainage, it is safe to assume that all are within the area of the residual mountain mass which rose above the peneplain produced in Miocene time; and that to this mountain haven the ancient population of *Shortia* became restricted.   Deep ravines with slopes affording suitable habitat must have been present in this area continuously since early Tertiary time and throughout the time of maximum extent

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[3] Such " wide range " does not imply continuous range in space ; it implies, rather, continuous in time but shifting in space, or sometimes splitting and diverging from a former ancestral site.   It is used in much the same way as " past range " shown by fossils, which may, usually does, represent different horizons.

of the peneplain.   Uplift and subsequent erosion have deepened
the valleys and doubtless have resulted in shifts in positions oc-
cupied by *Shortia*.   Recently, comparison of specimens from the
Keowee and from the Catawba drainage has disclosed " distinct
floral variations ", on the basis of which plants from the sources
of the Catawba River have been designated as var. *brevistyla*
Davies (65).   As the rate of evolution in *Shortia* has been very
slow (American and Asian species separated for geologic ages),
varietal segregation can be considered as indicative of a long pe-
riod of separation of the populations of *S. galacifolia*.   The geo-
graphic separation, although apparently not great, assumes a dif-
ferent light in view of a peculiarity of seed reproduction.   The
seeds germinate within the ovary; then the stem decays and falls
over (38, 159).   As *Shortia* grows in dense mats, the chance of
survival of seedlings so produced is small; only stems at the
margin of a patch would have much chance of coming in contact
with the soil.   Migration would be infinitely slow.   This interest-
ing plant can endure temperatures far lower than those experi-
enced in its native habitat; it has been grown successfully in New
Hampshire where temperatures of $-40°$ F. are recorded, and in
Quebec, 15 miles north of Montreal (116).   Its lack of an effec-
tive dispersal mechanism and its hardiness should be considered
in connection with persistence of " Miocene relics " in the South-
ern Appalachians throughout the cold phases of the Pleistocene.

No other Appalachian endemics have received the attention that
has been given to *Shortia*.   Yet there are other rare species and
many of more or less localized distribution which are mentioned in
the literature (29, 32, 33, 34, 38, 41, 84, 110, 112, 123, 162).
Diphylleia cymosa, of rich moist soil in the cove hardwood forests,
and *Buckleya distichophylla,* parasitic on the roots of hemlock, are
localized in the Southern Blue Ridge province; *Rhododendron
catawbiense, Stewartia ovata (pentagyna), Astilbe biternata* and
Clethra acuminata occur both in the mountains and along the rug-
ged western border of the Appalachian Plateau, but are absent
from the intervening area where the Schooley peneplain was best
developed.   *Galax aphylla,* the only species of its genus but with
related genera in Asia, has a comparable but somewhat wider dis-
tribution, including a number of outlying stations, some of which
are on the Coastal Plain (see discussion of diploid and tetraploid
races).

Some of the American representatives of genera of eastern American–eastern Asian relationship have their centers of distribution west of the Appalachian Highlands. *Cladrastis lutea,* most abundant in the Interior Low Plateau of Kentucky, and with disjunct occurrence in the Ozarks of southwestern Missouri and in the Southern Appalachians, is very closely related to *C. shikokiana* of Japan (123). *Cladrastis* is known to have been present in America in early Tertiary time (22, 25, 33).

A lesser number of species display relationship with southeastern Europe, or with southeastern Europe and adjacent Asia. The genera of woody plants (as *Cercis, Platanus*) are usually ones of more southern distribution than many of the holarctic genera. Pairs of species (vicariads) showing an American-European relationship are for the most part found among herbaceous plants (38, 83). Examples are *Hepatica americana* and *H. nobilis* (*triloba*), *Anemone quinquefolia* and *A. nemorosa,* which Fernald (83) says "are obviously related though perfectly distinct species and it is clear that they have long been geographically isolated". *Oxalis montana* and *O. acetosella,* distinguished as species by Fernald (86), are not separated by Hara (102) and only doubtfully so by Gleason (95).

The fossil record discloses that many of the genera now confined to America and Asia had representatives in Europe in pre-Pleistocene time (maps, 23), that Tertiary ranges included America, Europe and Asia. The widespread Tertiary ranges were interrupted by continental change (the breaking of land connections) and later curtailed by Pleistocene glaciation which killed out the European representatives of many genera. Within the continents physiographic changes correlated with erosion cycles brought about areal changes in vegetation, involving migration of species. Those of mountainous habitats were necessarily restricted to areas always mountainous. Thus the concentration of species of eastern American–eastern Asian relationship in the Southern Appalachians is explained.

The younger coastal plain area is strikingly different in vegetation and floristics from the older upland area. Although many of the more widespread species of eastern American–eastern Asian genera are present, many of the characteristic members of the flora of the Coastal Plain belong in "groups with wide tropical and subtropical range, the families, tribes, genera and sections

shared by the Americas with tropical and subtropical Africa, tropical and subtropical Asia, and Australia "(84). Examples are *Lachnanthes tinctoria* of the chiefly southern hemisphere Haemodoraceae; *Xyris,* a genus chiefly of the tropics and southern hemisphere. This should not be interpreted as meaning that no distinctive coastal plain species of American-Asian genera occur; some are present, as *Stewartia malacodendron,* belonging to a genus of eight species, two American (*S. ovata* of the Appalachian upland, and *S. malacodendron*) and six Asiatic (three in Japan, one in Korea, and two in central and eastern China) (123), and a family chiefly tropical in distribution (46, fig. 25; 95). *Croomia,* represented on the Gulf Coastal Plain by a local endemic (*C. pauciflora*), has two species in central and southern Japan (123). The endemic American genus, *Taxodium,* with *T. distichum* almost throughout the Coastal Plain in suitable habitats, has a long geologic record which shows that it once had Asiatic and European relatives, and that in early Tertiary time it was widespread in high latitudes (23).

The Coastal Plain, although relatively young geologically, nevertheless is the abode of many species of ancient lineage; of some, like bald cypress, whose past history is written in the fossil record; of some, like *Croomia,* whose past history is inferred from present distribution of relic species; of some, like *Stewartia malacodendron,* which may have been derived from ancient ancestors with tropical or southern hemisphere distribution and later became American-Asian in distribution; of some, like certain species of *Gaylussacia,* which seem definitely to be derived from South American relatives (see " Contributing Fields "); and of others, like *Lachnanthes,* whose relatives are chiefly tropical.

CONTINENTAL RELATIONSHIPS

In considering continental relationships it is necessary to recognize the principal physiographic areas of eastern United States, particularly the ancient Appalachian and Ozarkian uplands, and the Coastal Plain. Almost all papers dealing with floristic elements are concerned with one or more of these areas.

The flora of the ancient upland areas displays affinities with the floras of other sections of the American continent, especially with the Coastal Plain and the mountains of Mexico and Guatemala,

and to a lesser extent with the Tropics, the West and the North. The flora of the Coastal Plain, although with predominantly extra-continental affinities, contains floristic elements in common with the Appalachian and/or Ozark upland and in some cases the intervening Interior Low Plateau, and with the Great Lakes region. Disjunct distribution of species, of varieties or of related species or sections of genera illustrates the several types of geographic relationships.

UPLAND–COASTAL PLAIN AFFINITIES.   The Appalachian–Coastal Plain relationship was recognized at least 75 years ago, when Redfield (156) pointed out the surprising resemblance of the flora of Table Rock, N. C., to that of the New Jersey Pine Barrens. Later, Harshberger (112) elaborated somewhat on this idea and mentioned *Hudsonia montana* on Table Rock, related to *Hudsonia tomentosa* of the Coastal Plain and northern interior, and a number of plants of the high southern mountains which also occur on the Coastal Plain.   The Appalachian–Coastal Plain relationship was further stressed by Fernald (84) who pointed out that the relic colonies on the ancient and now uplifted peneplain contained plants of two categories: those belonging to tropical or austral genera (as *Lygodium, Xyris, Lobelia*), and those belonging to characteristic American endemic genera of the Coastal Plain (as *Orontium, Cleistes, Sarracenia, Hudsonia, Leiophyllum*).   Later, this relationship was shown to be well displayed by relic species and colonies on the Cumberland Plateau, where extensive remnants of the Schooley peneplain afford a variety of habitats— swampy flats and depressions, and sandy flats or knolls—persisting from the ancient low-lying surface (29, 30, 32, 33).   Bryophyte constituents of the coastal plain colonies of the plateau also illustrate the same sort of disjunction (167, 168, 171).

Disjunction of species range is illustrated by distribution maps of certain members of the Scrophulariaceae, as *Gratiola brevifolia, Tragiola (Gratiola) pilosa* (143); of *Cleistes (Pogonia) divaricata, Orontium aquaticum* (30); of *Uniola laxa, Panicum longifolium* (113); and by numerous floristic lists and by statements of range in manuals (29, 30, 33, 38, 86, 95, 171).   In some cases the disjunct pattern is more complex, and forms, varieties or related species are involved.   Examples are *Schwalbea australis* and *americana,* both of which are included in *S. americana* by Fernald

and by Gleason in the new manuals but are mapped separately by Pennell (143) ; *Habenaria blephariglottis,* with var. *blephariglottis* widespread and northern, var. *conspicua* in southeastern swamps and pine-barrens, and var. *integrilabia* in the relic coastal plain swamp communities of the Cumberland Plateau and on the Coastal Plain of Alabama and Mississippi (60, 86) ; *Leiophyllum lyoni* and *L. buxifolium* (41) ; *Sarracenia oreophila,* Appalachian relative of *S. flava; Sarracenia purpurea* var. *venosa,* with Appalachian stations in the Blue Ridge of North Carolina, and more extensive range across the Piedmont onto the Coastal Plain with separated areas on the Gulf slope and in New Jersey, in which latter area the widespread northern var. *purpurea (gibbosa)* arose (19, 207, 208, 209). A very rare and local endemic shrub of the western margin of the Cumberland (Appalachian) Plateau, *Conradina verticillata* (28), is very distinct from the other three species of the genus which are Floridian and Gulf Coast plants, a feature suggesting a long period of isolation.

In a study of North American pitcher-plants, Wherry (209) has mapped the ranges of all species and has shown by broken lines and arrows his interpretation of location of ancient stock and direction of migration to establish present range. All are interpreted as migrating from the ancient upland area as the Coastal Plain became available, or as being derived from ancient species of that upland. One species, *S. jonesii,* still inhabits a small disjunct area in the highland.

Pennell (143) has interpreted ranges of many species of the Scrophulariaceae as showing migration from ancient Appalachian upland populations; such interpretations are based on the presence of primitive characters. Of course not all species which occur on old and young land areas are so interpreted; he maintains that some have gone in one direction, some in the other.

It is rather generally agreed that the Appalachian–Coastal Plain relationship is in part a result of extensive peneplanation in Tertiary time (or Cretaceous, according to some authors), which favored the expansion of vegetation suited to a plain of low relief with swampy flats and depressions and intervening flat to rolling sandy soil areas (the underlying rock of a considerable fraction of the upland is sandstone). That is, what is now thought of as coastal plain vegetation occupied the peneplain. Uplift, with con-

sequent gradual dissection of the surface, curtailed the extent of suitable habitat on the old surface, while contemporaneously, gradual emergence of a coastal plain afforded comparable habitats which in part were populated by migration or spread from the old land area.   Continued dissection so greatly reduced the remnant areas of peneplain that disjunction of the plant population resulted. The small remnants of coastal plain vegetation (relic colonies), the disjunct occurrence of species and the rare endemics reflect this past history (33, 38, 84).   Cain believes that this " really is a question not of coastal plain plants in the Appalachian and Cumberland uplands, but of upland plants in the coastal plain, if we view the relationship historically ".   It is also suggested that cooling, resulting from uplift and later from Pleistocene ice advances, was a factor influencing migration of tender species to the Coastal Plain.   The " Hypothesis of Pleistocene origin of existing distributions " would interpret these coastal plain plants of the upland as recent (post-glacial) migrants.

The above type of distribution is one in which characteristic and often widespread coastal plain species occur as disjuncts on the upland.   The reverse pattern is also seen, that of upland (inland and Appalachian) species in local areas of the Coastal Plain.   This is particularly true of the hilly areas in northern Florida and adjacent Georgia (Tallahassee Red Hills, Marianna Red Lands, Apalachicola River bluffs, Eocene Red Hills, etc.), and the Tunica Hills of Louisiana, where in rich woods of ravines, many species which are not ordinarily seen on the Coastal Plain occur along with species limited to the Coastal Plain (35, 198).   Local endemics, some of them very rare and local, occur along with the inland species (see section on endemics), as do also varieties and subspecies (or more rarely species) related to Appalachian or Appalachian and Ozarkian species (as of *Asclepias,* 216, 217).   The widespread inland or Appalachian species are sometimes referred to as " northern disjuncts " (121, 122).   The inland species which reach their southern limits in Louisiana (for the most part not mountain species as stated by Brown (35) from Cocks (54) are believed by Brown to have persisted since early Wisconsin time because of favorable topography.   This hypothesis will not account for the local endemics nor the disjuncts of exacting edaphic requirements.   These all indicate a more ancient refugium.   It

has been suggested that the rare relic endemics, and other species perhaps derived from such relics, are " remnants of a widespread, mesic Tertiary vegetation which found refuge in northern Florida during periods of climatic stress " (198). Persistence since Tertiary time of the inland disjuncts on the Coastal Plain, together with the accompanying endemics, was made possible by the physiographic history of the areas (33). It is entirely possible, as Thorne suggests, that southward migrations of inland plants have been favored during the Pleistocene, thus augmenting the flora of the older relic communities.

The flora of the Ozark upland, like that of the Appalachian upland, has many representatives of ancient genera, a few of which are endemics or species of peculiarly disjunct range. Two of the endemics, *Castanea ozarkensis* and *Hamamelis vernalis,* have eastern as well as Asiatic relations; one, *Andrachne phyllanthoides,* is of tropical ancestry. A number of species of Appalachian or wide distribution east of the Mississippi River occur in the Ozark upland as disjuncts (33).

Coastal plain species also are present. Natural ponds, known as " sink-hole ponds ", occur on dry oak-hickory ridges and level uplands of the Ozarks of southern Missouri, and afford suitable habitat for coastal plain plants. Careful search of these areas during the past decade has resulted in discovery of a number of species not hitherto known to occur in the Ozark area (189, 190, 192, 194, 195). Although the number of such species is small—as would be expected because of the drier climate—the explanation commonly offered is the same as for coastal plain relics of the Appalachian upland. " These plants probably constitute one of the oldest recognizable elements in the present plant life of the region, harking back to conditions that prevailed before its last elevation in late Tertiary time " (140).

EASTERN UNITED STATES–MEXICAN AND –TROPICAL. Many of the genera of the ancient upland areas belong to families which include tropical and subtropical species. This is true of *Stewartia,* already mentioned as illustrating the eastern American–eastern Asian relationship. It is equally true of some of the commonest genera, as *Smilax* and *Viola.* Such relationships, however, are remote and indicate a long period of evolution from more primitive forms whose descendants are now localized in tropical or southern hemisphere latitudes to the more specialized forms of our area (46).

Closer relationships, comparable in nature to the relationships exhibited by American-European or American-Asiastic vicariads, may be found in the mountains of Mexico and Guatemala. There, in areas of older rock formations (in contrast to the younger coastal plain deposits and Pleistocene and Recent volcanic deposits), are found species common to eastern United States, varieties of our species, and also species closely related to those of eastern United States (134, 170, 191). The most conspicuous examples of identical species are trees. *Liquidambar styraciflua,* which at its lower altitudinal limits is associated with such tropical forms as tree ferns, at higher altitudes with oaks and such other eastern American species as *Carpinus caroliniana* and *Ostrya virginiana* as well as many subtropical species, some of which belong to familiar genera, is found in more of the stations studied along the eastern Escarpment of the Central Plateau and mountains of Guatemala than any other of the many identical species listed by Miranda and Sharp (134). As examples of closely related species, may· be cited *Fagus mexicana,* similar to beech in southeastern United States; *Magnolia dealbata,* similar to *M. macrophylla; Sambucus mexicana,* similar to *S. canadensis; Tilia longipes,* similar to *T. heterophylla.* Some species, listed as identical, are not always so considered (181). Varietal status is given to some taxa, for example, *Ilex vomitoria* var. *chiapensis* (173).

Comparable examples of relationships could be cited from ferns, mosses and fungi (166, 169, 172). Sharp considers that " many if not most of these so-called tropical bryophytes [of eastern Tennessee] are representative of a once widespread Tertiary flora ".

The family relationships are explained by Camp (46) as due to early origin of angiosperms, probably on southern hemisphere land masses, and " divergences of the basic, generalized familial groups . . . on this southern land mass certainly by the mid-Mesozoic ". He points out that " the great bulk of the angiospermous families (at least their woody members) and many of their present-day genera, appear to have evolved by the Cretaceous ". He believes that present distribution patterns point to the southern land masses as centers of primary evolution and centers of dispersal of evolving floras. Such an explanation means early occupancy of geologically old areas, with much more recent migration onto younger areas.

Miranda and Sharp (134) and later Sharp (174) point out the relation of the Eocene Wilcox flora of the Mississippi Embayment to the Mexican flora which contains, not only many of the Wilcox genera still known in southeastern United States, but also a considerable percentage of its more tropical genera. This implies the establishment of the vegetation of the Eastern Escarpment as resulting from southward shift of Eocene floras and perpetuation in these old land masses. Disjunction is attributed to the xeric nature of northern Mexico and southern Texas. Steyermark (191) emphasizes the importance of the geologically old mountain areas of Guatemala, not only as refuges for disjunct species of southeastern United States but also as the site of endemic species. He states that " the element of the flora of the eastern portion of the United States that reached Guatemala may have invaded that country at the end of the Cretaceous or early Tertiary when both regions were low-lying and peneplained, and previous to later uplifts ".

The many paired species and the more or less distinct varieties indicate a long period of separation—not so long, perhaps, as the American-Asiatic separation, for specific segregation is not so pronounced. It should be noted that none of the restricted species of the Southern Appalachians occurs in Mexico or Guatemala, that all the identical species are wide-ranging and that the United States representatives of paired species also are wide-ranging. Local endemics of those Latin American areas belong to genera unknown in temperate latitudes of America. They date far back in evolutionary history.

Basing conclusions on geologic features (163), Sharp (177) states that " the present temperate element in the flora of Mexico must have come from the north during late Pliocene and the Pleistocene " because, prior to the extensive faulting and volcanic activity of that time, much of Mexico was low-lying and unsuitable for temperate vegetation since the Cretaceous. In a recent analysis of floristic relationships between Mexico and the United States (71a), the suggestion is made that " the eastern North American plants . . . probably did not migrate southward into Mexico and Guatemala until the early Pleistocene ".

This hypothesis of late arrival of the temperate element is opposed to that based on the distribution of certain phylads which show a V-pattern and which have been explained (133) as due to

northeastward and northwestward migration from southern Mexico and Central America (see Contributing Fields). Although the eastern Cordillera and Central Plateau of Mexico are of relatively recent origin regarding elevation, it is entirely possible that the western Cordillera and land westward of the present coast of Mexico which has been down-faulted relatively recently was of sufficient elevation for the ancestral population of the temperate genera of Mexico. Migrations may have taken place both northward and southward.

It seems probable that a final separation or disjunction of the ranges of mesophytes would have been effected by the climatic barrier—a dry belt—which developed in the Pliocene. There is no evidence of opportunity for free interchange between the Mexican highlands and southeastern United States since the development of the grasslands in Pliocene time. Pluvial periods of the Pleistocene allowed " mesophytic elements in northern Mexico and Texas to meet their eastern relatives ", as shown by introgression in *Juniperus* (9, 99) and *Cercis* (9). However, such xero-mesophytes as *Juniperus* and *Cercis* are not comparable in moisture requirements to the disjunct mesophytes of the mountains of Mexico and Guatemala. The "warm-moist" interval in post-Pleistocene time indicated by the pollen profile of a Texas bog (150) permitted *Castanea* to extend a hundred miles beyond its present limit (at the same time that grasses and oaks were abundant) ; but does not seem to have been favorable to any appreciable proportion of mesophytes.

EASTERN UNITED STATES AND THE WEST. All authors treating the vegetation or floristics of the prairie States point out the western and the eastern elements in the flora. Such dovetailing of floras, well illustrated in Kansas (93), North Dakota (160), Missouri (140), Oklahoma and Texas, ordinarily does not involve pronounced disjunction and therefore will not be considered here. Relic prairie species and prairie colonies in the eastern deciduous forest are disjuncts commonly interpreted as a result of the post-Wisconsin " xerothermic period ". This phytogeographic feature will be considered in sections on prairie relics and persistence near the glacial border.

Disjunct identical species and closely related species of eastern United States and the far West are relatively few. *Polypodium*

vulgare, of Europe and western America, and *P. virginianum,* sometimes considered to be only a variety, illustrate a peculiar distribution pattern of closely related taxa (81, 83, 95). Ranges given in the manuals (86, 95) enable one to find examples of species of eastern range which also occur in California and/or other Pacific Coast states. Sharp (175) lists some of these when pointing out " relationships between the floras of California and southeastern United States ". Examples of identical species are *Agrimonia grypsosepala* and *Ranunculus pusillus;* of pairs of closely related species, *Dirca palustris* and *D. occidentalis, Pachistima canbyi* and *P. myrsinites* (in both cases, the only two species of their respective genera). The western species of *Dirca* is very local—restricted to an area 90 by 12 miles in the Oakland and Berkeley hills (183); the eastern species of *Pachistima* is local. McVaugh suggests that these very similar (or identical?) " species " of *Dirca* migrated long ago from an ancestral area in Mexico, that their distribution pattern is referable to the V-form shared by many phylads (133).

This East-West disjunction is explained by Sharp as attributable to the bisection of formerly continuous ranges, in the north by Pleistocene glaciation, in the center and south by a xerothermic period or periods, or by earlier events. In the case of such distinct specific segregation as displayed by the two species of *Pachistima,* the separation would seem to date back to late Tertiary time, if not earlier. *Pachistima* is an ancient genus, its presence in eastern United States dating back to the Ripley flora and late Cretaceous time (24). The peculiar disjunct range of the eastern *P. canbyi* (31, 128) also suggests the influence of events earlier than Pleistocene, as most of its stations are in the old (Tertiary) Teays drainage.

A few of the endemics of the Appalachian shale barrens have western relatives, as do also those of the granite flat rocks of the Southeast (see section on endemics). The rather distant relationship of eastern and western species of *Ranunculus* (see " Contributing fields of botany ") is said to date back to Tertiary time (20).

A number of species common to eastern and western forests (as *Viola canadensis*) are not disjuncts, but have a continuous range in a great northern arc around the interior grassland.

EASTERN UNITED STATES AND THE NORTH. The mountain ranges of eastern United States extend in a southerly direction

from the cooler latitudes of the Northeast. Hence the ranges of many species which are rather wide in the north extend southward along the mountains at increasing elevations as lower latitudes are reached. Many do not have even approximately continuous ranges in the mountains but instead appear here and there as disjuncts. The latter group is usually of greater interest to the plant geographer. A few examples of paired or vicarious species also fall within this general distribution pattern, as *Abies balsamea* and *A. fraseri, Diervilla lonicera* and *D. sessilifolia.* Outside of the mountains, which afford a climatic environment similar to that of more northern latitudes, some northern disjuncts occur as well as some with more or less continuous ranges but more abundant northward.

The spruce-fir forest of high elevations of the Southern Appalachians has been shown to be " distinct yet a part of the boreal forest formation " . Although it contains a number of species in common with the more northern forest, it has in all layers species not occurring in the North (139). However, the " northern affinity " is apparent in both physiognomy and floristic composition (37, 139).

Disjunct occurrence of northern species at elevations of the Southern Appalachians below the spruce-fir forest (37) and at widely separated localities throughout much of unglaciated eastern United States except the Coastal Plain (the " northern disjuncts " of hilly areas of the Coastal Plain are species widespread in the deciduous forest belt) has been noted by many authors (5, 17, 29, 33, 62, 71, 140, 143, 166, 167, 186, 192). Some of these note only occurrence and offer no interpretation; for example, *Betula papyrifera* on North Fork Mountain in West Virginia (5), *Spiraea latifolia* var. *septentrionalis* on Hawksbill Mountain, Page Co., Va. (17). Some relate the outlying southern occurrences of northern species to southward migration in the Pleistocene; for example, the isolated plant of *Taxus canadensis* in the Piedmont Province in Virginia is interpreted as " a likely relict from the Pleistocene " (71); the several species more or less isolated south of the glacial boundary in Missouri are considered to have migrated southward during the " Ice-age " and to have persisted in suitable habitats (140, 192). Others suggest the possibility of greater age; for example, in his monograph on the Scrophulariaceae, Pennell (143) states, concerning *Collinsia verna,* that " the range of the

species is very largely in glaciated territory, and it may be that such remote occurrences [more southern] . . . are relicts of a pre-glacial more southern distribution ", and of *Mimulus ringens*, that " this species, surviving glaciation presumably in the southern Appalachian upland, has so successfully reoccupied glaciated territory as to have its main present development thereon ". Woodson (217) interprets the range of *Asclepias exaltata*, which is predominantly within the glaciated territory, in like manner. He says that " being preadapted to the moist woods, meadows and copses of the northeast, *A. exaltata* has proceeded to migrate into them from its ancient refugium in the southern Appalachians ".

Tsuga canadensis, sometimes referred to as a northern species, is better thought of as an ancient Appalachian species, dating back to Tertiary time in the unreduced Southern Appalachians where its root parasite, *Buckleya distichophylla*, occurs (33, pp. 45, 481). Southern occurrences of *Pinus strobus* may well be explained in the same manner, as indeed may similar ranges of other species, even though such evidence as exists for *Tsuga* is not available. Neither hemlock nor white pine occurs at increasing elevations southward, as do the more distinctly northern species. Even at its southern limit in Alabama, hemlock is at a low altitude (106, 109, 165). Furthermore, hemlock is susceptible to frost damage. In an investigation of frost pockets in the High Plateau of western Pennsylvania (Kane Experimental Forest) it was found that hemlock was damaged " to a much greater degree than any of the hardwoods " and that 49 per cent of 291 hemlocks tallied in 1936 " showed evidence of past frost injury to terminal or side shoots " (114).

The occurrence of northern species of bryophytes in east Tennessee has been explained (166) as due to pre- or inter-glacial persistence. Later (167) it was suggested that " aggressive northern species not previously existing in the Southern Appalachians may have migrated southward and subsequently met one of three fates: (*a*) they may have later retreated northward, leaving no record in the south; (*b*) they may now have a continuous range to the north; (*c*) they may still be restricted or endemic in these mountains ". Steere (186) discusses the disjunct distribution of *Bryoxiphium*, pointing out the " similarity between the distribution of this species and that of many preglacial and interglacial relic

species of vascular plants "; he considers it an old species, a member of a once widespread flora.

It is apparent that there are two unlike interpretations of disjunct southern occurrence of now northern species: (*a*) that such species were in the north, moved south at times of advancing ice, then moved north again, leaving part of the population in isolated suitable habitats; (*b*) that such species were widespread in preglacial or interglacial time, their ranges curtailed or in some cases bisected by advancing ice sheets, and that some failed to move northward in postglacial time while others migrated into the glaciated territory. It seems probable that the first explanation fits some cases, the second explanation others, and that each species must be considered separately. (See also section on persistence near the glacial border.)

LOCAL FLORAS

In the foregoing classification of floristic affinities, by emphasizing the larger geographic areas of unglaciated eastern United States, papers concerned with relationships displayed by more or less local floras have been slighted.

The consideration of affinities of local floras was fostered by papers by Adams (2, 3) and by Kearney (117, 118) around the turn of the century, by some of Fernald's older papers, and by Cowles' lectures on geographic botany. A large proportion of such papers deal with floras in the glaciated area (for example, 80, 130, 142); some with borderline areas (141, 160, 197); a few with parts of unglaciated eastern United States (29, 37, 85, 122, 188). The general plan of treatment varies but little. Some classify the species as intraneous or extraneous, subdividing the latter into disjunct species and species at margin of range, and ally these with definite floristic areas or with floras to the north, the south, the east, and the west; i.e., they distinguish the various " elements " or " affinities " of the flora. Fernald, for example, classifies the species of the " inner Coastal Plain of Virginia " which are " restricted in occurrence " into 17 categories illustrating affinities with other geographic areas (85). Others are concerned with only one extraneous element, thus emphasizing a specific type of distribution (142).

Certain objections to what is termed a " synthetic approach "

in the analysis of local faunas and floras are stated by Deevey (66). However, the sort of conclusions he ascribes to data derived from " analyzable species "—such as the local area in question being a part of a larger region because the majority of its species " come from " that area—seem not to have been made in most botanical papers. Cain (40) defends the classification of floristic elements in the flora of a local area at the same time that he points out certain drawbacks.

PRAIRIE RELICS

From the time of the early settlers, mention has been made of prairie and prairie inclusions (often called " barrens ") within the forested region of eastern United States. The prairies of the Mississippi Valley, even the more or less disjunct prairies of the eastern part of the " Prairie Peninsula ", that lobe of prairie extending eastward into Ohio, seem much less out of place than do the more southern outliers ; they are in equilibrium with the climate, and in contact with bordering oak or oak-hickory forest (200). The prairies in unglaciated southern Ohio (26), in the northern district of the " Cliff Section " and in the " Knobs " east of the Bluegrass section of Kentucky are isolated prairie inclusions surrounded by more mesic forest types (33). In the Black Belt of Alabama and in Mississippi, prairie extends far eastward of the Mississippi River (33, 104, 107, 108, 124). The Barrens of western Kentucky form a great semi-circular arc following for the most part an area underlain by cavernous limestone and with poorly defined surface drainage (33, 129).

In floristic composition these prairie communities of unglaciated eastern United States resemble the prairies of the Prairie Region, but have in addition, a number of southern and Ozarkian xerophytes. They are, apparently, disjunct communities made up in large part of species displaying more or less pronounced disjunction of range. Thus in Alabama some of these prairie plants " are not found elsewhere in Alabama " (108). *Arenaria stricta* ssp. *texana* is an extreme disjunct in southern Ohio (27). Steyermark (193) separates the glabrous-leaved form of *Silphium terebinthinaceum* of these relic prairies as a distinct variety. Anderson (9) notes introgression of the Texan *Cercis reniformis* into *C. canadensis* as far east as southern Indiana and Ohio, where dwarf redbuds are frequent in prairie communities.

As some of the prairies located not far south of the glacial border may have resulted in part from migrations earlier than the post-Wisconsin " xerothermic period ", their further consideration is included in the next section of this paper. At the time that Gleason (94) outlined the probable vegetational history of the Middle West, the southern Ohio prairies that give evidence of influx from the southwest were unknown, and he thought that prairie had never encroached upon this area.

The post-Wisconsin eastward expansion of prairie is correlated with the time of the thermal maximum, the " xerothermic period ", which has been amply reviewed by Sears (164).

PERSISTENCE NEAR THE GLACIAL BORDER

The floristics of the glacial border presents problems unlike those of other areas. Often there is a motley assortment of " elements "—northern species, southern species, prairie species, local disjuncts, and endemics—assembled in localized areas and sometimes closely associated. Termination of range, not at the glacial border where there may be a distinct break in edaphic environment, but some miles south of it where no such break occurs, is a common phenomenon in the Middle West. Isolated occurrences of southern species near the border, and occurrence of southern species whose more or less continuous ranges stop 15–20 miles south of the glacial border while still abundant; disjunct occurrence in places clearly related to the preglacial or early interglacial topography; and border occurrences with stations neither to the south nor within the glaciated area—all are readily observable distribution features.

These features are usually interpreted as due to persistence of species or groups of species which entered during climatic phases of Pleistocene and Recent time unlike the present and which now remain as relic species or in relic communities, and of species which were part of the older pre-Wisconsin or preglacial vegetation (27, 33, 34, 201, 213, 214). The " Glacial Border " symposium of the Ecological Society reviews many of these features (73).

Among the early advocates of persistence not far south of the glacial border were Adams (2), Transeau (199) and Harshberger (111, 112), all of whom believed that the conifer forest belt along the ice margin west of the Appalachians was very narrow. Harshberger thought that " the glaciers did not effect the true

distribution at any great distance from the ice front " and that conifers occupied " the outer rim of tree vegetation during the glacial period ". The mixed forest " south of the arctic tundra vegetation, was a remnant of the great Tertiary forest " which " persisted during the period of refrigeration with its greatest denseness in the region drained by the Tennessee River and its tributaries " and whose northeastern tongue extended well up into southeastern Pennsylvania, while " in the Ohio Valley, the streams flowing from the south during the glacial period would aid in preserving the broad-leaved mesophytes, as far north, as the Ohio River ". Gleason's idea (94) was quite comparable, for, with reference to the five floristic groups of plants of the Middle West which lay outside the margin of Wisconsin ice (the prairie flora, the Ozarkian forests, the coastal plain flora, the deciduous forests of the Appalachians, and the northeastern coniferous forest), he states that " there is no reason to believe that the general space relation of these five groups has ever been altered, although they must have suffered many fluctuations in their dis-tribution and extent during the preceding glacial advances ". He considered that the coniferous forest was " reduced to a narrow strip between the ice margin and the deciduous forest ". These expressions of opinion dealt with vegetation.

Basing conclusions on pollen profiles in bogs within the area of the Early Wisconsin drift and in the southern fringe of the Late Wisconsin drift, where a pronounced spruce-fir maximum per-sisted for a long time, Potzger (147) believes that in the Ohio-Indiana-Illinois area there are indications of " a wide belt of co-nifers south of the glacial border, which broadleaved species had not replaced before advance of the ice sheet known as Late Wis-consin "; and that the presence of pollens of these trees in a Texas bog was further indication of such a band.

Termination of range of species near a glacial boundary, and persistence of plants in suitable habitats in remnants of their former ranges are beliefs early fostered by Gleason (94) and Fernald (82).[4] " If a considerable number of species are now confined to an area immediately beyond a moraine and seldom occur within

[4] Fernald's discussion is so well known and has been so often reviewed that it needs no further mention here, particularly as it treats of areas beyond the range of the present review.

it ", three explanations may be offered: (*a*) " present conditions of soil and climate may exclude them "; (*b*) " their migration up to the present time may have extended merely to the moraine, which they will later cross "; (*c*) " they occupied this area before or during the formation of the moraine, have occupied it ever since, and are not at present extending their range ". After weighing the first two in the light of field observation, Gleason accepted the third explanation, not alone for distributions along the front of the last, but of earlier glaciations as well, and in support of which he mentioned a number of southern species whose ranges terminate in southern Illinois, although a strip of similar habitats extends northward up the Mississippi. Of course the first explanation fits many species, but when climate and edaphic factors are similar on both sides of the line, it must be ruled out. The second will fit some species, " but it is difficult to understand why the boundary of the range of numerous species should be so nicely adjusted to the moraine ". There are many species, both plant and animal, whose ranges are thus nicely adjusted, as distribution maps will show (34, 196).

Persistence does not always involve termination of range; in many instances the site is notably disjunct, or local endemics are involved. Such is the case in the Driftless Area, of which Fassett (74) writes: " This distinct relic flora, practically confined to The Driftless Area, with several endemics, having its affinities in unglaciated areas to the westward or to the southeastward, may be clearly interpreted on the basis of lack of glaciation in southwestern Wisconsin ". The species of *Sullivantia* are among the best of examples used to illustrate persistence. Four of the six species are in the Rocky Mountains; *S. sullivantii* (*S. ohionis*) occurs locally near the glacial border in Indiana and Ohio, with one Kentucky station, while the related *S. renifolia* is a species of the Driftless Area and occurs in two places in east-central Missouri just outside the glacial boundary—which here is the boundary of old drifts, Kansan and Illinoian (26, 27, 33, 34, 74, 192, 214). The apparent explanation is early disjunction of range of ancestral stock followed probably by migration of the separated parts, and evolution of the isolated races. Disjunction of range of *S. renifolia* appears to be an event of Illinoian or even an earlier time. The peculiar habitat (with " grotto microclimate ") of this

species and *S. sullivantii* would certainly favor survival near the glacial border. *Dodecatheon meadia* var. *frenchii*, which has a range comparable to that of *Sullivantia renifolia*, occurs "in the Driftless Area and extreme southern Illinois, seeming to be a relic of a preglacial expansion of *D. Meadia*" (78). It also occurs in Kentucky, in the same area as *Sullivantia* and other disjuncts. The moss, *Bryoxiphium norvegicum*, is an old species, "undoubtedly a member of a once widespread flora which extended over the northern hemisphere in late Cretaceous or early Tertiary times", and whose range was disrupted by glaciation, leaving relic stations in Iceland, Greenland, Washington, the Driftless Area, along and south of the Wisconsin glacial border from Missouri to Pennsylvania (186). Many decided disjuncts and peculiar assemblages of species occur in parts of the ancient Teays drainage system in Ohio and northeastern Kentucky, and have been interpreted as preglacial and early glacial relics (33, 196, 201, 213).

Direction of migration and degree of relationship of populations of a species, such as may be determined by mass collection studies, sometimes lead to dating of isolation of a fragment of the population—as of the Indiana population of *Rubus odoratus*—where the relation to other populations is distant and leads to "the assumption that the isolation of *R. odoratus* in unglaciated southern Indiana greatly antedates the postglacial migration of that species into New York and New England" (75). Further consideration of such studies is better included in the next main section of this review.

Relic communities, isolated segments of vegetation unlike the surrounding vegetation and not successionally related to it, except as stages of one clisere may obliterate those of another, also occur. Most conspicuous of these are the boreal and prairie communities.

The boreal communities are readily interpreted as relics of the retreating migration of the more northern vegetation which once fringed a glacial margin. The age, however, may not always date from Wisconsin glaciation but may be earlier, as is evident from the preceding discussion of species ranges.

Prairie communities south of the glacial boundary are variously interpreted. They may be remnants of the eastward migration of prairie in post-Wisconsin time through what is now referred to as the Prairie Peninsula (200); they may be pre-Wisconsin or even earlier, perhaps augmented by post-Wisconsin migrations (27, 34). Several features contribute support to the latter hy-

pothesis: many of these prairie communities are more xeric than those on the Wisconsin drift in the area of the Prairie Peninsula; they contain a large number of species (about 150 have been listed), most of which are common to the western prairie and prairies of the Prairie Peninsula, and in addition, species absent from the Prairie Peninsula which occupy xeric habitats southward (as *Agave virginica*), and species which have evidently come from the south and southwest (see section on Prairie Relics). The southern xerophytes, the decided disjunction of southwestern or Ozarkian xerophytes, the distribution of such species as *Asclepias viridis,* whose range is said to be of great age (217), and as *Leavenworthia uniflora* (16) which do not extend across the glacial boundary, and the varietal differences in *Silphium terebinthinaceum* and perhaps in other species, as well as community relations, suggest that the separation of these prairie communities from the great western prairie may not have been contemporaneous with the post-Wisconsin eastern expansion of prairie, but may have been consummated at an earlier date (34). Such features indicate a spread of xeric elements, not from the prairies of the Upper Mississippi Valley but from the Ozark region and southward.   These prairies are the communities referred to by Deevey (66) as " patches of a xerophytic (*Andropogon scoparius–Bouteloua*) type of prairie community, containing no western elements, but instead coastal-plain elements such as *Agave virginica* and *Ophioglossum Engelmanni*" which misrepresents the statements made in the literature cited.   Neither were these " patches " said to be " northwestern outliers ".   Frequent use of the word " patch " implies small size, whereas some of these prairies were hundreds of acres in extent.

The question arises—can all of the floristic features of the glacial border be explained as post-Wisconsin and due to existing or recently operating environmental factors?   It appears that workers familiar with the field aspects of the problem believe that they cannot; that the " occurrence and local distribution of the biota cannot be understood simply by analysis of climatic, edaphic, and biotic factors of the environment on either side of the boundary at a point in time, but that they must be interpreted also in the light of the history and inheritance of the organisms themselves in relation to this history of the soils and land surfaces " (155).

What reasons, based on vegetation alone or existing conditions,

are there for believing in the possibility of persistence? We might turn to the "nunatak hypothesis" in its modified form. At high latitudes today plants grow at the borders of the Greenland ice-cap (1), and on spots completely surrounded by glaciers—on nunataks in the Greenland ice-cap where scattered plants are found (1), and at altitudes of 4100 to 6000 feet in the Fairweather Range of Alaska where little patches of flowers and "turf-banked terraces" occur (56). At much lower latitudes (38°–40° N) temperatures must have been much less extreme, even at the maximum of continental glaciers, than at the margin of the Greenland glacier today, length of warm season longer, angle and intensity of sun greater. Consequently it may be expected that a greater variety of species could have survived. It appears "not impossible that we now have in the region of the glacial border species whose ranges of tolerance are or were sufficient to allow them to survive the periglacial climate with its attendant instability of soil" (155).

The great range in temperature in microclimates of different habitats of a limited area enters into the problem of persistence. A difference of 39° F. in minimum temperatures has been recorded for unlike sites in one small area near the glacial border in Ohio (215). The distribution of such species as *Sullivantia sullivantii*, which at its southernmost station occurs near such northern relics as *Taxus canadensis* and *Acer spicatum*, suggests persistence since an early Pleistocene ice advance. So also does the distribution of *Dodecatheon meadii* var. *frenchii*. The distribution of *Styrax grandifolia*, of *Pachistima canbyi*, etc. also suggest persistence from early Pleistocene. On the other hand, some patterns of distribution are clearly related to Wisconsin and post-Wisconsin climates.

The floristic features of the glacial border are intimately associated with the question, "How far-reaching were the effects of glaciation?" to be considered later.

ENDEMICS OF LOCAL OR PECULIAR HABITATS

Local endemics and pronounced disjunction of range have always received the attention of phytogeographers, as has been apparent in several of the topics already considered. The absence of close relatives of some of our local endemics raises question as to their time and manner of origin. Concentration of endemics in

local and sometimes peculiar habitats, and association with these of pronounced disjuncts of various affinities, make it desirable to consider such concentrations of species apart from the topics above.

Although little has been written about Alabama endemics, that State, nevertheless, contains two interesting endemic species —*Neviusia alabamensis* and *Croton alabamensis*—which, although not in the same habitat, are in the same geographic area, the Warrior Coal Basin and Upper Cahaba Valley. The former is a member of a monotypic genus of the rosaceous tribe Kerrieae which contains, in addition, two closely related Asiatic monotypic genera, *Kerria* and *Rhodotypus*. It is hardy as far north as southern Ontario and Massachusetts. The latter belongs to a very large genus of chiefly tropical distribution and best represented in the Americas; it is an evergreen shrub of tropical aspect. *Sedum nevii* from two counties in Alabama—with *Croton* in one locality and with *Neviusia* in the other—differs in chromosome number from Virginia plants which are now called *S. glaucophyllum* (53). Two species, only slightly different morphologically, are represented in the complex, the Alabama one with a $2n$-number of 12, the Virginia one with a $2n$-number of 28 (13). The rare endemic, *Croomia pauciflora,* is here also, and, although it belongs to a genus with two Asiatic species, these are southern in distribution, and members of the family (Roxburghiaceae) range through tropical Asia and Malaysia to tropical Australia. A subspecies of the black cherry (*Prunus serotina* ssp. *hirsuta*), which possesses " the features which may reasonably be assumed to be ' primitive ' in *Prunus serotina*", is now localized in this area and in the hilly Gulf Coastal Plain area to be considered next (132). *Cotinus obovatus* (*C. americanus*), of extremely disjunct range and most abundant in western Texas, occurs farther north in Alabama.

The significance of such endemic and disjunct species was recognized over half a century ago by Mohr who wrote of these as " the slightly modified descendants of types belonging to an ancient flora, which have survived the changes our globe has undergone and have found a refuge in their present localities " (135). Obviously the relationships and distributions are such that distinct floras seem to be represented. The chromosome situation illustrated by *Sedum nevii* and its derivative supports the belief in a

refuge somewhere in the southern Appalachian Plateau of Alabama.

In one of his essays, Asa Gray immortalized one of the most striking and rare endemics of the Apalachicola river bluffs, a hilly area of the Gulf Coastal Plain—*Torreya (Tumion) taxifolia* (162). This genus is represented in Upper Cretaceous deposits of the Atlantic slope (21); "there are no records in the long interim, but somewhere through the 60 million years, representatives of the genus lived on, giving rise (on the American continent) to *Torreya taxifolia* of Florida and *T. californica* of California" (33). Li (123) lists four Asiatic species. Another even rarer endemic of this same area, *Taxus floridana,* belongs to a genus with a similar history, and with a similar but wider range, especially in north-temperate latitudes. This species of *Taxus* certainly should not be called a "northern disjunct" as suggested by Deevey (66); to do so seems to put emphasis on the genus rather than the species, which the same author states should be dealt with. It would appear that the ancestors of both species had persisted somewhere in the Southeast, perhaps over considerable area, but were finally restricted to areas which survived late pene-planation (Coosa) and Pleistocene submergence. A number of other endemics, as well as many inland species with disjunct ranges, occur here also. (See Upland–Coastal Plain affinities.)

Woodson (216, 217), using biometric studies in *Asclepias,* demonstrates the probable antiquity of a Floridian refuge which he calls "Orange Island". This he considers one of three major refuges—Appalachia, Ozarkia, and Orange Island—which "were available to the biota of the southeastern United States during the late Mesozoic and early Cenozoic", and upon which "the modern speciation of *Asclepias* is considered to have developed". Orange Island is the richest of the three refuges in endemic species and subspecies of *Asclepias.* The three subspecies of *A. tuberosa*—all of which are panmictic—could not have maintained separate existence in contact with one another, and are used to show that the three populations arose from a common ancestor independently and in isolation.

The lower Altamaha River in Georgia is known as the last refuge of *Franklinia alatamaha,* first discovered on October 1, 1765, and last seen in the wild state in 1790. Its habitat and history of

discovery, together with possible causes of extinction, have been discussed (103, 204), but its possible route and time of entry are in doubt. It is one of the more advanced members of the Tea Family, whose species are mainly tropical and subtropical; genera exhibiting the more primitive characters are represented in South America, the probable southern hemisphere land mass from which ancestral expansion took place (46). One of the widely separated localities for *Leitneria floridana* is the lower Altamaha River; this is the only representative of a family of doubtful relationship.

Outcrops of granitic rock in the Piedmont of southeastern United States, which are known as " Flat-Rocks " or " Cedar Rocks ", " are without parallel in eastern North America and support a remarkable and more or less endemic flora " (131). These rock exposures vary in extent from spots but a few meters across to areas of hundreds of acres; some 6000 acres of rock are exposed in Georgia alone. Of about 200 species definitely identified with the flat-rocks, 44 are considered as the most " typical " or " characteristic ", and more than one-third of these (17 species and varieties) are endemic on the flat-rocks, i.e., "they occur in nature on these exposures only "—a high degree of endemism or near-endemism for a small area. The occurrence of two species of monotypic genera, *Diamorpha cymosa* and *Amphianthus pusillus,* each with no near relatives in its family, and of a third, *Sedum pusillum,* sometimes separated as a monotypic genus, emphasizes the phytogeographic interest of the flat-rock flora.

" If the complete geographic ranges of the most typical members of the flat-rock association are mapped, it at once becomes evident that almost all the plants in question, if not confined to the flat-rock habitat, are Coastal Plain and Piedmont species which have affinities with species of the Mississippi Valley or of the Ozark Region or even of the western United States and Mexico ". This points to the possibility of an element of the Piedmont flora being derived from semi-arid regions of the Southwest and of the Mexican highlands. The extreme antiquity of establishment of the group is indicated by the unique species and genera, and is dated as later than the Cretaceous seas which separated eastern and western North America and probably in Tertiary time or later. Its failure to invade the Blue Ridge is explained as due to the occupancy of that area by ancient mesophytic forest.

Based in part upon a study of weathering of the granite, of "weather pits" in the granite, and of failure of soil accumulation, the rocks are interpreted by McVaugh as being of great age, hundreds of thousands or perhaps millions of years. "The flat-rocks have not had any general covering of soil in recent geologic periods, and possibly have never had such a covering since the last general peneplanation of the Piedmont surface" (131). On the other hand, Oosting and Anderson (138) relate the origin of these exposures to factors which produced the Fall Line but believe that certainly there has been sufficient time for the development of a complete cover of vegetation. They also believe that "it is not unreasonable to suppose that at one time the rocks were completely covered with at least sufficient soil to support a meager forest" and that "with the advent of the white man, lumbering, fires, and erosion might well have exposed these areas where the rock was nearest the surface". They were noted by William Bartram in accounts of his travels in 1776 before any extensive activities of the white man in that area. Successional evidence indicative of possible closure of vegetation over the rocks is used in the one case (138); in the other, geologic evidence of rate of weathering, coupled with the peculiar geographic ranges of endemic species and the absence of any close relatives of three of these endemics (131). It would seem to be necessary that exposed rock surfaces had been continuously available within the general granite flat-rock area since the beginning of speciation of the endemics. It would also be possible, even probable, that at times some rocks became covered by a thin mantle of soil, only to be exposed again by windfall and/or erosion; that the slow succession which has been outlined (119, 138) occasionally culminated in the development of a shrub or even forest cover which could be easily destroyed by windfall or fire.

In the Cedar Glades of the Nashville Basin of Tennessee, where flat surfaces of Ordovician limestone are exposed, a number of endemic and near-endemic species occur. The vegetation of this interesting area has been described by several writers, and some of its species listed (105, 151, 152). Cytological investigation of the species of *Leavenworthia*, all four of which occur in the Cedar Glades of Tennessee, which is the center of variability for the genus, are enlightening. Only one species, *L. uniflora*, ex-

tends far beyond the confines of the Nashville Basin. *L. aurea* appears to be the oldest member of the genus " because of its southernmost occurrence, disjunct range, and lower chromosome number ".   It is suggested that the basic pattern of this complex " is a reflection of glacial influence and of topography of the Nashville Basin, which since mid-Pleistocene has been favorable for the establishment of many populations . . ." (16).   The genus *Lesquerella,* with four species in this area, has its largest concentration of species in Texas and northeast Mexico, and is abundantly represented in intermountain areas of the West.   It is suggested " that representatives of both genera migrated from the southwest into the Nashville Basin ", there producing a number of distinct species (157).

The mid-Appalachian shale barrens of Virginia, West Virginia, Maryland and Pennsylvania have long attracted the attention of botanists because of the unusualness of their flora and particularly because of their endemic species (6, 11, 58, 59, 145, 185).   The shale barrens occur particularly on slopes on the Brallier shale (a very resistant noncalcareous shale) and afford habitats more or less unique in the East.   The endemic species and varieties of these shale barrens include some closely related to surrounding species of other habitats and not always recognized as distinct taxa, e.g., *Allium oxyphilum* and *Convolvulus purshianus;* some definitely distinct but whose relationships are evident although in certain cases remote; and one, *Pseudotaenidia montana,* which is the only representative of its genus.   *Eriogonum alleni* and *Senecio antennariifolius,* with related species in the Rocky Mountains, are interpreted as derived from Rocky Mountain species or from an ancestral species which gave rise to the now separated eastern and western species (205, 206).   *Trifolium virginicum,* related to the prairie species, *T. reflexum,* has a postulated origin in the Great Lakes area (206).   *Oenothera argillicola* has some characters in common with western species, and in some respects is more like certain eastern species; its chromosome arrangement differs from both (183), and there are indications of different races on different barrens (145).   The time of origin of the endemics has been variously interpreted: of *Eriogonum,* that its ancestors " crossed the continent and came down the Alleghenies during pre-glacial times, but subsequent climatic changes destroyed all trace of them,

leaving behind this single endemic species " (205); of *Senecio,* that the Tertiary ancestor of the Appalachian and Rocky Mountain species " grew somewhere in what is now central Canada " and that the descendants had migrated " far enough to escape the Quaternary ice sheets " (206); of the six species with relatives in the surrounding area, and probably the others as well, that " these plants evolved in their present habitat " and " since the last ice age " but perhaps from progenitors which had come in sooner (145). This last author bases his conclusions (*a*) on the fact that the endemics are well adapted in structure and physiology to shale barren conditions which he has determined by thorough field and laboratory investigation, and (*b*) on the belief that it " is unlikely that these barrens could support during the last ice advance the existing endemic flora, since the terminal moraine is less than 300 miles from the northernmost barrens ". As all of the endemics and near-endemics are geophytes or hemi-cryptophytes, it is difficult to understand why one would believe that the winters during the cold phases of the Pleistocene should have been so severe at 300 or more miles from the ice as to eliminate such species if they were already there. Using a genetic approach, Stebbins (183) believes that " the plant association of these barrens appears rather to have been gradually built up over a long period of time through the addition at widely separated intervals of plants derived from very different sources ". Not all the shale-barren endemics are confined to outcrops of Brallier shale; it is suggested that absence of competition in such open areas is a factor in determining the present distribution of the species (210).

CONTRIBUTING FIELDS OF BOTANY

Certain fields of botany whose contents are not ordinarily associated in our minds with plant geography yield data valuable in the interpretation of distribution patterns. Chief among these are evolutionary studies which give information on rate of evolution and speciation, evolutionary trends, and migration routes or shifting of floras; cytology and genetics, giving information, through chromosome and hybridization studies, of probable time of origin of taxa, of migrations and relationships; certain types of monographic studies; and biosystematy (48, 49), or the newer systematics with its study of " species as populations of living organ-

isms ", and the tracing of clines and probable migrations with the aid of mass collecting methods or population sampling.   The physiology of organisms, often expressed as tolerance range, must enter into interpretations of plant geography.   Although few investigations have been made of length of day requirements of wild species (4, 137), there is more than a possibility of this being a controlling factor in some cases.   Overlapping of various fields of botanical research is evident and their interdependence inescapable.   The possible contributions of genetics and cytology to floristic plant geography were pointed out briefly by Raup (154), and the relations of several fields were discussed by Cain (38), to whom the reader should refer.   A few citations from the more recent literature of these fields are illustrative; no attempt has been made to assemble a bibliography.

The great age of, and slow speciation in many of our common genera and genera to which some of our Southern Appalachian endemics belong are well known.   Paleobotanic and distributional data are used in making estimates of comparative rates of evolution.

Evolution of angiosperms has been going on since some time prior to the Early Cretaceous, the time of " the first reliable record of their occurrence ", which was in rocks of that age in Greenland. " Some of the fossils suggest an extended pre-Cretaceous history. Leaves of *Platanus* show no recognizable distinctions from those on living trees " (51).   Stebbins (184) believes " we should expect to find periods of rapid evolution alternating with times of relative stability. . . . And this is precisely what has occurred ". Four periods of rapid evolution are pointed out; the first of these was in Cretaceous time, the second " occurred throughout the world in the middle and latter part of the Tertiary ", and " the third accompanied the advance and retreat of the successive Pleistocene glaciations ".   A fourth, just beginning, is the result of man's alteration of the earth's surface.   Most of this evolution is on a relatively small scale.   It was during the first of these that many of our modern genera became differentiated.   In the second, speciation resulted in the establishment of modern forms and of the stock of closely related modern forms; the eastern American-eastern Asian relationship dates from this time.   In tracing the developmental trends of leaves of *Quercus*, Chaney (51) states:

" The genus *Quercus* is represented by an abundance of leaves which show a trend toward increasing size and lobation to the middle of the Tertiary period. Judging from these foliar organs there has been little if any evolution among the oaks since the Miocene epoch . . .". Very many of our tree genera were more diversified in Miocene time than at present and more widespread (23).

The fossil record of the Pleistocene, at least as far as tree species are concerned, is largely but not entirely a record of existing species; some species have become extinct. This is particularly true in Europe (23). " The evolutionary changes during this epoch were less than those of the previous periods of rapid evolution for two reasons ". The new climates were not greatly different from the climates of northern and alpine areas of pre-Pleistocene time, and the new habitats were poor in nutrients. Hybrids, and particularly polyploids, were favored, " so that evolution during the Pleistocene might be expected to involve chiefly allopolyploidy " (184).

The relation of cytogenetics to plant geography is illustrated by the statement: " One important generalization which undoubtedly holds good for the bulk of polyploid complexes . . . is that the polyploids are dominant in regions which have been only recently opened to occupation by plants, or which have been subjected to great climatic or other environmental changes, while the diploids tend to occupy the older, more stable habitats " (182).

The localization of diploids in old areas is illustrated by *Galax aphylla,* which has two chromosome races, a diploid and a tetraploid. Examination of the map showing distribution of chromosome races (12) reveals the interesting and perhaps significant fact that all plants examined from the Cumberland Mountains (including the southern extension to Lookout Mountain), the Allegheny Mountains, the western margin of the Cumberland Plateau and the Unaka Range along the Tennessee–North Carolina line were diploids; i.e., only the diploid race occurs in the area of maximum development of the Mixed Mesophytic forest climax, which is interpreted as the ancestral forest type of the Deciduous Forest (32, 33). In the Blue Ridge (in the limited sense, i.e., eastern range of the province by that name) and adjacent mountains and on the Piedmont, both races occur, while

only the tetraploid has moved out almost to the coast on the Coastal Plain in Virginia, i.e., onto a young land area.   Other comparable examples follow: *Sedum ternatum,* whose diploid race " has been found in a relatively restricted area in southern West Virginia, southwestern Virginia, and eastern Kentucky " [i.e., in the ancient Cumberland Mountains and southern Allegheny Mountains (and contiguous mountains of the Appalachian ranges)] has a tetraploid race which radiates out from that area in all directions (14).   *Sedum pulchellum* has a diploid race " in the western and southern parts of the specific area ", in Missouri, Arkansas, Oklahoma and Alabama northward into Tennessee (i.e., in the area of ancient Ozarkia and the southern Appalachian Highland) and a tetraploid which has spread northward into extreme southern Illinois and the Bluegrass section of Kentucky (15).   The situation in *Diospyros virginiana* is somewhat more complex: " a continuous distribution of the 60-chromosome race in the central and southeastern [older] parts of the specific area; a peripheral . . . of the 90-chromosome race . . ." (18).   The basic number " appears to be 15 ".   *Diospyros* is an ancient genus, 17 forms described from mid-Cretaceous rocks, known in the Eocene (?) of Panama, and now widely distributed in the tropics (23). This suggests that *D. virginiana,* the only species in our range and one whose tetraploid race has a range comparable to that of the diploids mentioned above, was long ago derived from a diploid ancestor of perhaps still more southern range.   The aneuploid *Sedum nevii–Sedum glaucophyllum* complex and the *Leavenworthia* complex have been referred to in the section on endemics.

The very complicated situation in *Vaccinium,* where diploid, tetraploid and hexaploid species and many hybrids have been observed in the wild, has been investigated by Camp and his co-workers (43, 44, 45, 63, 64).   The studies are for the most part a combination of cytogenetics and biosystematy.   The genus is thought to be very old, and probably was highly differentiated in the Cretaceous.   " The fundamental evolution apparently takes place on the diploid level and must be an exceedingly slow process " (43).   " Morphologically, some of the basic, diploid blueberry species are so different that one is almost tempted to consider the group to have more than one line of descent; certainly, if they have diverged from a common ancestral stock, it must have

been fairly early in the Tertiary " (64). Several indications of age can be mentioned: the great diversification, which has resulted in segregation of subgenera (or genera according to some classifications); pronounced disjunction in some of these, for example, *V.* (*Hugeria*) *erythrocarpum* " has a homolog in China " (45), the vine-like *V.* (*Herpothamnus*) *crassifolium* of " restricted areas from southeastern Virginia to South Carolina . . . has much in common with a few South America species which are mostly epiphytic, pendant, lianae-like plants " or at higher elevations grow in soil (45). The longevity of individuals of some species of *Vaccinium* is remarkable, a factor which favors chance cross-pollination and persistence of individual plants " in advantageous microhabitats in the face of ecological changes "; one clone of *V. myrsinites* is calculated to be not less than 1000 years old; clones of the distantly related box huckleberry (*Gaylussacia brachycera*) may have " persisted for untold thousands of years, at least since the late Pliocene or early Pleistocene " (63). In contrast to the slow evolution at the diploid level, " speciation among polyploids may be relatively rapid, being, in part, a phenomenon of the current scene " (43). But some polyploids are old. Hybrids are numerous, and " it is likely that as many interspecific hybrid blueberries have been naturally produced in the last hundred years [after the advent of white settlers and the clearing of forests] as in the preceding ten thousand years. However, . . . certain natural populations (e.g., *V. corymbosum*), which today are widespread, are the result of mass hybridizations during and after the Pleistocene, the result of readjustments along the distributional margins of several homoploids, following large scale climatic and ecological disturbances " (63). The conclusions reached in the several papers on *Vaccinium* here cited are based upon extensive field and experimental-plot studies; they have led to interpretations of geographic distribution which are dynamic. These papers should be referred to in connection with statements made in the " Hypothesis of Pleistocene origin of existing distributions ".

Introgressive hybridization, or " the gradual infiltration of the germ-plasm of one species into that of another as a consequence of hybridization and repeated backcrossing " (9), is apparent in many species populations and frequently gives evidence of past shifts in the ranges of species. This is particularly true of allo-

patric introgression, for it is introgression between species native to different areas. It can occur when and where species of these different floras come into contact because of climatic or geographic changes. Floras of the Southwest show frequent evidence of introgression because pluvial periods of the Pleistocene allowed mesic floras to expand and come into contact. On the other hand, species of the generally mesophytic East were not so affected, except toward the southwest. As a result of this, introgression along the Ozark-Texas axis is apparent in species so far analyzed which have a related taxon in that direction. Some introgression in eastern species comes from related taxa in the " Orange Island " Floridian area, in the Rocky Mountains (rarely effective in our area), in the North and occasionally from higher altitudes in the eastern mountains. Variability due to introgressions " is least perceptible in such floristically stabilized areas as the central interior plateaus of Kentucky and Tennessee " (9). Examples of variability due to introgression are: *Cercis canadensis,* introgression from the xeric *C. reniformis* of Texas and Oklahoma; *Phytolacca americana,* showing, in the Southeast only, introgression from the Caribbean *P. octandra; Juniperus virginiana,* unmodified in the central part of its range but showing introgression from the Southeast, the Southwest, the West and the North, with the northern race extending south on the Coastal Plain to about South Carolina; and sugar maple, also showing a mixture of species from several directions (9, 61, 70, 99, 100). All such research is based on study of variability in populations and analysis of the variable characters.

Monographic studies often yield significant data concerning relationships and probable antiquity of species or groups of species. The genus *Ranunculus,* well represented in most floral areas of North America except the prairie and plains grasslands, can be used as an example (20). " The Eastern Forest Flora is characterized by compact endemic groups of species with relationships to groups occurring in several directions. The high percentage of endemism indicates the antiquity of the probable separate invasions of the prototypes of these groups ". Certain of the species and their varieties (*R. septentrionalis, R. hispidus, R. carolinianus, R. fascicularis*) " are connected with their Pacific Northwestern relatives . . . by a chain of mutual relatives occurring

across the southern part of the continent ". Relationships indicate that the origin of this southern group of species may have been in Mexico or on the Pacific Coast, or possibly in the East, and that the migration was in Oligocene or Miocene time. *R. recurvatus* is related to and perhaps derived from a group now restricted to the Pacific Region. The wide-ranging *R. abortivus* may be the prototype of an aberrant group of a section of the genus (Epirotes) not otherwise represented in the East. Absence of members of this section "in the Northern Coniferous Forest is explained by the lack of aggressiveness of the section or its apparent inability to fill in the areas denuded by glaciers in the Pleistocene epoch ".

It is becoming increasingly apparent that many problems in taxonomy and phytogeography can be approached by means of mass collecting and study of populations, their degree of variability and the direction of increase or decrease in the intensity of variable characters. The last may give evidence of direction of migration and sometimes of time of isolation or of migration (47, 70, 75-79, 161). Thus in a study of *Rubus odoratus,* the isolation of a southern Indiana population which differs from all other populations of the species studied, is assumed greatly to antedate the postglacial migrations into New York and New England which took place from the unglaciated area to the South and whose direction is indicated by progressive changes from West Virginia to Maine (75). A study of beech, based primarily on extensive population samples, has shown that three distinct basic types of beech are present, each with somewhat different ecological requirements. But in some places " the population is genetically highly complex ". This condition is frequent in the area of late Pleistocene deposits, i.e., in the Beech-Maple Forest Region, and may account for the diverse ecological niches occupied by beech in this area (47). With the completion of this work we will know more about the probable time and course of migration of beech, and, by inference, of many other widespread but complex " species ".

" A revision of the North America black cherries " (132) is of phytogeographic interest because it suggests time and place of origin of subspecies of *Prunus serotina.* Analysis of morphological characters points to certain features which are primitive

and which define the hypothetical ancestor of early Cenozoic or late Mesozoic time. A subspecies, *hirsuta,* with the ancestral characters is "now localized in two areas in the Southeastern United States—areas, it should be noted, which support numerous other relict endemics like *Neviusia alabamensis, Croton alabamensis, Croomia pauciflora,* and *Torreya taxifolia*". This is similar to a southwestern taxon, ssp. *virens* var. *rufula,* which also has primitive characters. Migration of the early forebears of *P. serotina* was from tropical or subtropical latitudes northward "on both sides of the North American continent, possibly during the Mesozoic". Distribution of *hirsuta* suggests its separation from the primitive stock at an early date. The widespread ssp. *serotina* is much more recent and "seems to have interchanged genes with the original populations wherever contacts were made". Therefore, if isolated populations of *hirsuta* had always been surrounded by *serotina,* they could hardly have maintained identity. The distribution of the complex is in the form of a V with apex in Central America. This distribution pattern is common to many phylads ("phyletic lines of closely related species") and suggests south to north migrations, sometimes with intervals of migration in the opposite direction (133).

VEGETATION PATTERN AND CORRELATION WITH PAST EVENTS

The present pattern of vegetation is the result of existing conditions of climate and local environment and of past conditions—extent and configuration of land, erosion cycles, climate and glaciation. Just as taxonomists recognize refuge areas and probable migrations, and point out the significance of endemism and disjunction, so must the ecologist delve into the past in an attempt to explain the present. From the great mass of material on the geology, paleontology and physiographic history of unglaciated eastern United States, certain facts and events may be selected which are necessary to an understanding of plant distribution and vegetational development.[5] Into this brief chronological account are woven references to the floristic relationships already discussed, thus coordinating the whole into a series of related events.

[5] These have been discussed by the writer much more fully in Part III of "Deciduous Forests of Eastern North America" (33) than can be done in this review.

A contrasting interpretation, which places great emphasis on the Pleistocene, will follow the more generally accepted history here outlined.

MESOZOIC HISTORY

The significant history begins with the Great Appalachian Revolution at the close of Paleozoic time. The Appalachian Highland then assumed something of its present area; the Interior Highlands (Ozark and Ouachita provinces) finally emerged from the sea. Beyond a doubt, these uplands were occupied by a land flora.

During the early Mesozoic era, reduction of the mountains and plateaus formed by the Appalachian Revolution began. A pre-Cretaceous peneplain—the Fall Zone peneplain—was produced, and after subsidence was covered by Cretaceous sediments. The so-called "Cretaceous peneplain" of many earlier writers is younger than Cretaceous. West of what is now the Interior Highlands, a vast epicontinental sea extending inland from the Gulf of Mexico effectively cut off this land area from the far western lands which extended southward into Mexico. An Ozarkian-trans-Pecos "peninsula" extended southwestward from the more eastern land mass. By the end of Cretaceous time this peninsula was connected with the land to the south in Mexico. For the most part the Cretaceous continent was low-lying and very different in outline from the present continent. The more or less V-shaped distribution patterns of many phylads, with the base of the V in Mexico or Central America, may have been initiated at this time (see Contributing Fields).

Botanically the late Mesozoic era is marked by the appearance of angiosperms in the fossil record of America, their rapid increase in numbers, and great expanse in area. From the beginning of the record in America some forms referable to living genera were found. The common ancestor of the four present-day subspecies of *Asclepias tuberosa* is believed to have existed in Cretaceous time (217). By the end of this era the modern aspect was apparent, and many genera of the deciduous forest—as *Quercus, Juglans, Fagus, Celtis, Sassafras, Liriodendron*—were represented in deposits of the Atlantic slope or Mississippi Embayment. Modern as well as ancient and now extinct genera of gymnosperms were also represented, as *Picea, Pinus, Thuja* and *Tor-*

reya (*Tumion*).   The progenitors, then, of some of our common
and widespread species, as well as of some of local and apparently
relic distribution (as *Torreya* and *Pachystima*) were known in
the flora of what is now southeastern United States.   The climate
was mild (spruce in these earlier deposits is not considered to be
indicative of a cool climate), and without marked zonal differ-
ences; rainfall was abundant.

TERTIARY HISTORY

A significant feature in the physiographic history of the Ceno-
zoic is the gradual emergence of the Atlantic Coastal Plain.   Old
areas (the Cretaceous continent of Paleozoic and earlier strata)
and young areas (the emerging coastal plain) were separated by
differences of the edaphic environment.   To some extent such en-
vironmental differences must have influenced the development of
a vegetation cover and the distribution of species during at least
the earlier part of the ensuing Cenozoic time.   Granite outcrops
may have been exposed on the Piedmont, and if so, must have
been populated by plants capable of adapting to the peculiar local
environment (see granite flat-rocks in section on endemics).   Up-
lift also initiated the Schooley cycle of erosion which culminated
in Miocene time.   Farther west, a water barrier of Paleocene time
probably extended northwestward from the Mississippi Embay-
ment to North Dakota and adjacent Alberta (the Cannonball Sea,
marine sediments), temporarily cutting off Ozarkia from the East.
In the Western Interior gradual draining of the epicontinental sea
of Cretaceous time allowed vegetational expansion—well recorded
in the fossil record of that area.

These events of Tertiary time were of great importance vegeta-
tionally.   The erosional history is recorded in land forms still re-
taining something of their mid-Tertiary configuration and in other
features related to that erosion cycle.   The distribution pattern of
major vegetation types, the relationship of species and subspecies,
disjunction of ranges, and localization of endemics should be ex-
amined in the light of Tertiary history.   The undissected expanses
of the Cumberland Plateau, with their swampy depressions, are
but slightly lowered remnants of the Schooley (or Cumberland)
peneplain.   Here are the disjunct occurrences of coastal plain spe-
cies of ancient ancestry.   The knobs and rounded hills (monad-

nocks) rising, sometimes a thousand feet above the peneplain level, are the abode of endemics and disjuncts. In the Southern Appalachians (southern Blue Ridge Province of physiographers), mountains several thousand feet in height remained—this area was not in Tertiary time reduced to peneplain status, and in this always unreduced area is the greatest concentration of endemic species with eastern Asian relatives. The western escarpment of the Appalachian Highland, and all other places where resistant rock outcropped, retained some topographic diversity. Here, too, are local endemics and disjuncts of ancient ancestry. The Coastal Plain gradually enlarged and became available to species migrating from the uplifting peneplain as well as to those entering from lower latitudes. The Mississippi embayment was reduced in size, but its alluvial sediments continued to present a barrier to free interchange of upland species at the same time that it afforded easy means of migration toward the interior.

While this erosional history was in progress, suitable sites for the preservation of plant remains occurred along the Atlantic and Gulf coasts and in the Mississippi embayment (the Paleocene Midway and Eocene Wilcox formations). Many genera with modern representatives in eastern United States were represented in the abundant Wilcox flora, as *Aralia, Asimina, Cercis, Liquidambar, Magnolia, Taxodium.* For the most part these are genera which by modern standards are thought of as having southern affinities or as best represented in lower latitudes. Representatives of many now tropical or subtropical genera were also present. The common genera of more northern latitudes—which were conspicuous in Upper Cretaceous floras—are lacking in Eocene deposits of southeastern United States, but continued on in the Western Interior and the Arctic, and, because of the higher elevations of the Southern Appalachians, probably remained in that area also. The fossil record is from lowland sites of deposition, and, as MacGinitie (125) has pointed out, it is difficult to determine the nature of upland forest; remains of upland plants are extremely scarce; species represented by the more abundant fossils probably grew near the site of deposition. Although much of the eastern American continent of mid-Tertiary time was low-lying, highlands were present and doubtless supported a flora differing from that of the lowlands.

The fossil record indicates a mild climate, perhaps warmer than that of Cretaceous time, and this, together with the growing connections with lands of lower latitudes, afforded opportunity for great shifts in floras and for infiltration of genera from southward. Also, Tertiary land connections in high latitudes, at the time of mild climates in the far north, account for the Asiatic and European relationships displayed by so many American plants, while reduction in extent of areas of great relief accounts in large part for the localization of Southern Appalachian endemics.   Also, we find that the finest examples of Mixed Mesophytic forest climax—lineal descendant of the mixed Tertiary forest—are in areas where the Schooley peneplain was never perfected (the unreduced areas).   The central position of this forest climax in the vegetation pattern is thus accounted for.

With uplift and warping of the Schooley surface, streams were given renewed cutting power, and a new cycle of erosion, the Harrisburg,[6] was initiated.   Peneplains began to develop in many separate drainage basins, but never coalesced because of lack of time. Areas underlain by resistant rock were dissected but not greatly reduced.   Continuation of, and even expansion in area occupied by mesophytes was possible.   Distribution patterns of species and of forest types probably assumed something of their present form. The mountainous Southern Appalachians remained a haven for species restricted by the Schooley cycle of erosion.

The alternation of ridges and valleys which characterize the topography of the Ridge and Valley Province was then brought about.   The infertile and thin soils derived from the resistant and often steeply dipping strata of ridges is, and doubtless was, favorable to the development of the Oak-Chestnut forest climax, as a derivative of the ancient mixed forest.   Shale barrens must have been produced, and evolution of some of the species of the present barrens may well date from this time (see Appalachian shale barrens in section on endemics).   The Piedmont was peneplained, only to be dissected again, thus exposing or enlarging granite outcrops.   The Interior Low Plateau was formed but doubtless retained hilly areas where the mixed forest could survive.   Erosion in the Interior Highlands reduced much of the land to peneplain

[6] For discussion of varying interpretations of peneplain age, see Braun, 1950, p. 494.

status, favoring the persistence of species of coastal plain swamps, but left two rugged areas (Boston and Ouachita mountains) where relic mesophytes could survive. The enlarging coastal plain of Late Tertiary time approached the present Coastal Plain in extent. Some hilly areas remained, as they doubtless had in the previous cycle, thus permitting continuance, in these sites, of species of the mid-Tertiary flora.

The fossil record of the late Tertiary—the time of the Harrisburg cycle of erosion—is very poor, both in the Southeast and in the Western Interior. The flora of the Gulf Coast resembles that now found there. In the Western Interior, increasing aridity (due to continued rise of land which first drained off the epicontinental seas and finally culminated in the uplift of the Rocky Mountains) is reflected in the nature of the fossil remains. Eastward retreat of the more mesic elements of the flora, or, toward the west, restriction to the more hilly areas, doubtless took place. The Oak-Hickory association was thus derived and came to dominate the Ozarkian area. The xeric western and southwestern element noted in the flora of the granite flat-rocks may have entered at this time. The map of distribution of *Asclepias* (*Asclepiodora*) *viridis* (217), which is considered to be a species " probably of great age ", suggests this as a possible time of entry into southern Ohio and adjacent Kentucky.

The Harrisburg cycle was terminated by uplift in late Pliocene time. Ensuing erosion cycles have had no far-reaching effects, although they have produced a few local features affecting species ranges; for example, the Nashville Basin in Tennessee, with its " Cedar Glades "; the Coosa peneplain on the Gulf slope, and above which rise groups of low hills with their disjunct and endemic floras.

PLEISTOCENE HISTORY

A discussion of Pleistocene events may seem out of place in a review concerned with the phytogeography of unglaciated eastern United States. However, a knowledge of Pleistocene events and effects of glaciation is essential to the interpretation of the vegetation of the unglaciated area.

Glacial stages (times of ice advance) alternated with interglacial stages (times of ice retreat). During the former, great quantities of water were locked up in the glaciers; as a result,

sea-level was lowered and the shore line was seaward of the present coast; during the latter, sea-level was raised and the low-lying coastal plain was partly submerged.   Sea-level is known to have varied as much as 400 feet, exposing more or less of the continental shelf when at lower levels, flooding the land when high. New land for plant occupancy and migration was exposed during each recession of the ocean.

The " glacial boundary " is a composite line, here following one, there another of the great ice sheets.   At no time did glaciers cover the entire area within the " glacial boundary ".   In a peripheral band the land surface was modified by outwash deposits, ponding of streams and drainage changes.   Farther from the ice front, topography was unmodified except by normal erosional processes, or locally by deposition from overloaded streams fed by melting glaciers.

The last or Wisconsin glacial stage is divided into four substages, between which there were partial withdrawals of the ice. The ice of the last of these substages (Mankato) did not reach as far south as earlier advances.

The fossil record of life in Pleistocene time is meager.   A few plant fragments (leaves, fruits, seeds, wood, and rarely stumps in situ), mosses and pollen occur in organic deposits of interglacial stages and tell something of the vegetation north of the glacial boundary in these interglacial times.   Carbonaceous lenses in Pleistocene terrace deposits of the Atlantic and Gulf coasts and Mississippi embayment contain some plant remains, but exact age of most of these deposits is doubtful.   Pleistocene deposits along Little Bayou Sara in Louisiana, where stumps of *Taxodium distichum* and *Nyssa sylvatica* (or *aquatica*?) occur, are of particular interest because of the admixture of northern and southern species—*Larix laricina* (wood), *Picea glauca* (wood, twigs, needles, cones), *Thuja occidentalis* (small fragments of branches), together with such southern species as *Taxodium distichum, Chamaecyparis thyoides* (small piece of wood), *Diospyros virginiana, Quercus* spp., and many widespread species (red cedar, walnut, hickories, beech, tuliptree, boxelder, cucumber-tree). This has been explained by stating that the northern element dovetailed into or telescoped into the warm-climate vegetation, and that each occupied suitable sites (35).

All macro-fossil deposits indicate persistence of an occupying

vegetation comparable to that of today, and an infiltration of more northern species. Pollen records tell another story which must be correlated with dating of deposits.

DATING OF DEPOSITS. Many million years have elapsed since the beginning of angiospermous vegetation in America, and about one million years have passed since the first continental glacier started its advance.

In a chapter on " Pleistocene Chronology ", Flint (87) has reviewed the various methods used in attempts to ascertain the length of time since glacial retreat from certain areas. Among these are rate of recession of falls, rate of sedimentation on deltas and on lake floors, rate of accumulation of peat, rate of precipitation of travertine—in all of which a number of variables are involved. Varves have been used with considerable accuracy in limited areas, although errors may arise in making correlations from place to place (10).

Attempts to estimate the lengths of glacial and interglacial stages of the Pleistocene are generally " based on comparison of the progress reached by some process, such as weathering or general erosion, during some stratigraphically known time, with the progress reached by the same process in postglacial time within the same region " (87). Depth of leaching of soils and amount of material lost by erosion have been used in several places. Such calculations are based on an assumed 25,000 ± years for the amount of time since the last (Mankato) Wisconsin ice maximum.

Measurement of radioactivity of residual Carbon 14 in organic remains is the latest method being used in the measurement of postglacial time. Measurements made at the Institute for Nuclear Studies, University of Chicago, and at the Lamont Geological Observatory of Columbia University appear at intervals in Science. Some of these measurements, such as those made from wood or peat in glacial deposits, are of particular interest for the phytogeographer (see Radiocarbon Dates (153) in Bibliography). For example, the age of a sample of peat from Singletary Lake, N. C., is given as " older than 20,000 "; cypress wood buried under sand deposited by the Santee River in South Carolina is " older than 17,000 ", and cypress wood from Myrtle Beach is " older than 20,000 ", which would appear to date back at least as far as Cary time. On the other hand, the age of peat from Cranberry Glades,

W. Va., is 9423 ± 840 years; from Cedar Bog Lake, Anoka County, Minn., 7988 ± 420 years; of wood and peat from the Two Creeks forest bed in Manitowoc County, Wis. (by far the most interesting late-glacial deposit known; see section, "How far-reaching were effects of glaciation?") is approximately 11,000 years (figures range from 10,877 to 12,168). All of these are of the same order of magnitude, and all are Mankato or post-Mankato (153). All are notably less than estimates arrived at by previous methods.

Under the title of "Radiocarbon dating of late-Pleistocene events", Flint and Deevey (88) have brought together much of the significant material of the short period of radiocarbon investigations. For the purposes of this review, their most significant statements are: "The time of attainment of the Boreal type of climate, i.e. the time of the pine zone, differed appreciably according to the latitude of the locality. The pine zone is about 9,000 years old in West Virginia, about 8,000 years old in Connecticut, and about 6,000 years old in Maine; it is about 8,000 years old in southern Minnesota and about 7,000 years old in northern Minnesota. The age of the thermal maximum (climatic optimum) has not been precisely fixed, but several samples from horizons not far from it give ages ranging from about 6,000 to about 3,000 years ago".

The radiocarbon measurements give more definite dates than have hitherto been possible; they demonstrate a shorter time interval since the Mankato maximum than has previously been postulated. Thus the reconstruction of events in late-glacial and postglacial time should be correlated with these recently ascertained dates. A limitation of the method has been that it could not be applied satisfactorily to material older than about 12,000 years; however, recent advance in technique (153) "permits dating back to 30,000 years".

THE POLLEN RECORD. The pollen record of late-glacial and postglacial time is one of the chief sources of information concerning migration and the development of vegetation within the glaciated area. South of the glacial boundary, pollen records are few and often incomplete. Most of them contain some spruce or fir at the lower levels, indicating some infiltration of northern genera; most,

but not all, show considerable agreement with existing surrounding vegetation. When spruce is present, this fact is always emphasized, but the presence, at the same level, of pollen of trees of more southerly range is seldom mentioned, although it may be as reliable a climatic indicator as is spruce.

No attempt is made here to review the literature on pollen profiles, for that is beyond the scope of the present review. Only those of particular phytogeographic interest will be considered. Most significant are the pollen profiles from a Texas bog, from bogs in the New Jersey Pine Barrens and from the Carolina bays (depressions in the Atlantic Coastal Plain).

The features of greatest significance in the 22-foot Texas pollen profile are " the presence of pollens of *Abies, Picea glauca, P. mariana* and *Castanea* ". The first three of these are essentially confined to the lowest levels, and total only silghtly more than two per cent of the 1450 pollen grains in eight of the foot-levels. The last (*Castanea*) occurs almost throughout the record; it is present with spruce and fir at some of the lower levels, and reaches a maximum about two-thirds of the way toward the top. The limit of its present range is 100 miles to the eastward. " Climatic changes suggested by the vegetation are: cool (boreal conifers), to warm-dry (*Quercus* and grasses), to warm-moist (*Alnus* and *Castanea*), to warm-dry (*Quercus, Carya,* grasses), becoming still drier towards the topmost level in the bog " (150).

Pollen profiles from bogs in the New Jersey Pine Barrens not far south of the glacial boundary show a " total lack of a successional trend in the forest history ". They suggest " a highly mixed forest cover in which northern conifers were associated in a minor way with southern broad-leaved genera " and seem to justify the conclusion " that unglaciated New Jersey was during Wisconsin times a refugium for southern broad-leaved trees, with intrusions of the association by such boreal genera as spruce and fir " (146, 148).

Recent studies in North and South Carolina afford the most complete information yet available (90–92). These have the advantage of radiocarbon dating of certain horizons. In the pollen diagrams of eight cores taken from " bays " in the southeastern portion of the North Carolina Coastal Plain, pronounced vegetational changes are recorded. The record is said to begin with

early Wisconsin, probably Iowan, time and extend to the present. *Picea* is present in small amounts at all levels older than about 10,000 years (radiocarbon dating), and it is of interest to note that *Liquidambar* and *Taxodium* were often present at the same levels as *Picea* and in comparable amounts. A pine-spruce maximum at a depth slightly greater than that of the dated horizon is believed to be of Mankato age. Size of the pine pollen indicates that it was not one of the species now on the Atlantic Coastal Plain. Increases in the pollens of broad-leaved mesophytes are believed to be contemporaneous with interglacial subages. Frey believes that if the forest of the Southern Appalachians " was perhaps displaced only to somewhat lower elevations, then one might expect that a substantial occurrence of hemlock, elm, hophornbeam, and perhaps beech, at the present locations [Carolina bays], would be correlated with a glacial advance, or in other words with a maximum depression of climate. This is contrary to the present findings ". It appears from the diagrams that occurrence of the above-mentioned mesophytes is contemporaneous with occurrence of sweet gum and bald cypress, and large amounts of oak and hickory, a combination not unlike that occurring on parts of the Coastal Plain at the present time. No adequate explanation is offered for the pine-*Isoetes* maxima of the Cary and Mankato subages, when mesophytic trees and higher aquatics are almost absent except in the overlap to adjacent horizons, and bog shrubs and sphagnum greatly reduced. Such a flora might indicate lowering of the water table so that the lake level was reduced to a silt flat covered with shallow water and hence favorable for a prolific growth of *Isoetes* with perhaps a border of bog shrubs, and the surrounding forest was too dry for most broad-leaved trees. As an objection to such a xeric hypothesis, Frey notes the presence of peridinians, a part of the microfauna. An alternative explanation involving local deep burning of the peat and redistribution of peat through erosion has recently been advanced (203). Any fire which burned out the peat of the bog would doubtless have extended through surrounding forests; dominance of pine can be brought about by fire. " Climatic fluctuations undoubtedly occurred, correlated with advances and retreats of the Wisconsin ice sheets. Purely by inference at this time it is believed that the climate at more inland locations also varied during this period and

that the climax forests of these locations probably experienced considerable displacements " (92).

The North Carolina pollen profiles present a number of problems which have not yet been solved. They show that there were pronounced fluctuations in vegetation near the coast, but they can give no indication of how far inland such changes occurred. They suggest that at no time during the Wisconsin age did Appalachian forests move near enough to the coast to affect the pollen record; if they had, surely the dominant chestnut, with abundant windborne pollen, would have been recorded. Considering the edaphic requirements of most of the species of the cove hardwoods, they could scarcely be expected near the coast.

The evidence derived from pollen profiles must be considered in connection with all other sorts of evidence bearing on the phytogeography of eastern United States.

AN HYPOTHESIS OF PLEISTOCENE ORIGIN OF EXISTING DISTRIBUTIONS

An unusual viewpoint, one very different from that held by the majority of plant geographers, and which brings the influence of the Pleistocene into great prominence, has been expressed by Edward S. Deevey, Jr. (66). It is based upon the fact that the Pleistocene has intervened since the species arose " in the Pliocene, or earlier ", and upon the belief that " there has been sufficient time, and sufficient transfiguration of geography, for the pre-Pleistocene distribution pattern to be completely transformed in a very large number of cases ". This is the thesis of a lengthy paper on the " Biogeography of the Pleistocene ", in which its author states that " documentation follows at some length ". This " documentation " is largely a matter of reinterpreting the works of many authors, sometimes with the original material so distorted that it is scarcely recognizable. A great deal of the literature used is zoological, but only the botanical topics are included here.

Deevey believes, as do many biogeographers, " that existing ranges of species and of larger groups are the product not of existing geographic conditions but of all geographic conditions obtaining throughout the history of the species or stock ", but that it certainly should not be assumed " the existing distribution pattern of the species to be as old as the species itself, or as the genus or

family to which it belongs ".   He feels that " most or all of [certain curious disjunctions of distribution] are explicable in the light of postglacial climatic changes ".

As a working basis, several " principles " are set forth.   One of these is, " We deal with species, not with families or orders ". Another, called the " Economy of hypothesis ", is of particular interest to all concerned with plant geography, for it states: " No distribution is taken to be old unless it can be proved not to be young . . . .   All distributions of species are taken to be of Pleistocene date in the absence of good proof that they are older ".   One may well ask, what constitutes proof?   Deevey further states, in connection with " Origin of species ", that " nearly all well-studied cases of subspeciation and speciation point to the Pleistocene as the time of such previous isolation, and the occurrence of related forms in the same area is therefore attributed to post-Pleistocene alterations in geography and in biogeography ".

The present knowledge of glacial and postglacial stratigraphy and fossil floras of North America is said to be inadequate; the stratigraphic detail of most deposits has not been worked.   Whether such interglacial floras as those described by Steere (187) and by Rosendahl (158) represent all or part (and what part) of an interglacial subage, is not known.   On the other hand, great strides are being made in postglacial stratigraphy, with the help of pollen analyses.

A brief résumé of postglacial pollen chronology with comments on the Xerothermic Interval and glacial refuges offers suggestions which need serious consideration in connection with other interpretations.   Pertinent are the discussions of evidence of a tundra belt, of the migration of certain tree species, of the somewhat more northern range limits of certain trees in the Xerothermic Interval, and of conditions south of the glacial boundary.

The existence of a tundra belt has been reported in Aroostook County, Maine, on the evidence of a large amount of grass and sedge pollen at lower levels of the bog profiles (68).   However, it has been pointed out (149) that pollens of sedges, alder and ericads, together with spores of mosses and ferns, characterize tundra, not pollen of grasses.   Lack of evidence of a tundra belt is explained (66) as probably resulting from the fact that the basins, which later became occupied by bogs, were filled with

stagnant ice long after the main body of the glacier had retreated and until a less northern type of vegetation had surrounded the basin. It is claimed that the belief of most plant geographers that the tundra belt in the Middle West was very narrow is based mostly on negative evidence. However, evidence based on fish distribution is said to suggest that " a subarctic tundra zone must have followed the retreating ice front across the northern United States and Canada . . . but the tundra must have been very narrow and impermanent, and the modern flora and fauna immigrated astonishingly early ".

" Pollen analysis has not been very helpful in establishing the location of refuges. In fact, as evidence accumulates that boreal forests were widely developed in the southern United States at about the climax of the last glaciation, it is becoming increasingly difficult to imagine a place where the characteristic components of the temperate flora could have taken refuge ". Nevertheless we find statements about "beech, moving out from its center of refuge in the northern Appalachians " during an early warm interval of postglacial time, and " hickory, moving eastward from centers of refuge in the middle West " during the ensuing warm dry interval, the Xerothermic Interval. The pollen sequence reflects phytogeographic movements. The evidence for " widely developed boreal forests " is based upon pollen and macro-fossil deposits already discussed (see Pollen Record), all of which are in a peripheral position as far as deciduous forest is concerned, and in locations (except the Texas bog, in which *Castanea* was contemporaneous with *Picea*) where it is possible or even probable that adjacent bodies of water, cooler than today, tended to lower summer temperatures. Deevey places great weight on the pollen of the Texas bog and on the plant remains in Little Bayou Sara deposits in Louisiana because " members of the northern Coniferous forest community occurred during the Pleistocene " as far south as Texas and Louisiana, which he believes means that, " unless one can believe that the typical temperate species were pushed south of the Rio Grande and deep into peninsular Florida, the alternative is a picture of an extraordinary intermingling of boreal, temperate, and subtropical elements along the Gulf coast (and on land now submerged along that coast by a postglacial rise of sea level) ". In neither case does the fossil record show any sub-

tropical species to have been present—the assemblage is one of deciduous forest species with an admixture of coniferous forest species; those of most southerly distribution (*Taxodium* and *Nyssa aquatica*) now range northward to southern Indiana and southern Illinois but are most abundant in the South; the magnolia is *M. acuminata,* which now ranges from Oklahoma, Louisiana and Georgia northward to the high Allegheny Plateau of northwestern Pennsylvania and western New York. Comparable assemblages are not uncommon today; for example, bogs in southern and western Connecticut where the southern white cedar (*Chamaecyparis thyoides*) and the northern black spruce (*Picea mariana*) sometimes occur together (136); the Carter Caves and Tygarts Creek forest in northeastern Kentucky where northern disjuncts (as *Taxus canadensis* and *Acer spicatum*) and Appalachian species of southern range (as *Magnolia tripetala*) occur together (33, pp. 111, 479).

The topic " Southeastern United States during the Pleistocene " is replete with material that needs critical examination. The area seems to include all of eastern United States south of the glaciated area, and is much more extensive than usually included in the Southeast.

The eastern American–eastern Asian relationship already discussed is pointed out, and animal and plant examples are mentioned. " There are various reasons for believing that the biogeographic connection implied by such disjunctions is old. Chief among these are the numerous instances where paleontologic evidence is available, showing that the present ranges are fragments of a formerly more continuous distribution ". The few cases of specific identity among plants (none is known among animals) are attributed to low rates of evolution. This would account also for the slight varietal differences displayed by many plants of eastern American-eastern Asian range. " In general, then, the biota of the southeastern United States is dominated by a large number of relicts of the Arcto-Tertiary forests, which had their floristic origin in the Cretaceous, were holarctic during the early Cenozoic, and gradually withdrew into the tropics in response to slow and interrupted cooling of the northern continent ". Dominated by relicts that withdrew into the tropics—and came back again? Many Eocene genera of the Wilcox flora did withdraw to the tropics and now

compose a considerable fraction of that flora, and many seem to have remained in temperate latitudes. Because latitudinal shifts of floras are demonstrable for early Cenozoic time, certain implications are believed to be involved: " Pleistocene climatic changes were more drastic than those of the earlier Cenozoic and accelerated the extinction of some stocks and the permanent withdrawal of others into the tropics. In addition, the present picture of Cenozoic climate and life suggests that the whole assemblage of species now living on the northern continents (and in the northern oceans) is of Pleistocene origin. It is difficult to see how cold-climate . . . plants can have arisen except under a climatic regime at least as glacial as today's ". But we know, from instances of specific identity or slight varietal differences of American and Asian species, that many of our species antedate the Pleistocene by several epochs. If it were not that these statements come under the heading, " Southeastern United States ", one might suppose that arctic and subarctic species were referred to, but this is not the case. The southern Appalachian and coastal plain floras are included in the material that follows. As the Southern Appalachians have long been " supposed " to harbor old relicts, Deevey feels that the question of " suitability of the Appalachians as refuges for ancient species during glacial stages of the Pleistocene " must be reopened. This is done by taking up and reinterpreting the works of others, and in some cases changing some of their basic statements.

The complicated problems connected with hybridization in *Vaccinium* (43) are brought into the picture. Referring to the three species (*V. arkansanum, V. simulatum, V. australe*), which gave rise to *V. corymbosum,* the statement is made that " Camp supposes that in pre-Pleistocene time these three species had parallel but not contiguous ranges essentially as today ". Camp states that " there is evidence that they arose from different sets of diploids probably no later than the mid-Tertiary during an early period of active speciation resulting from the geographical rearrangement of diploids ", and goes on to explain what he believes, as a result of long-continued research, brought about the final synthesis of *V. corymbosum.* But Deevey believes that " this is no doubt an unnecessarily complicated hypothesis; presumably one glacial age would accomplish what seems to Camp to require

several" and that "the fragmentation of ranges that led to the production of the older species, assuming it also to be of Pleistocene age, implies a considerable history of Pleistocene geographic changes *deep in the nonglaciated territory*". Camp believes there is evidence for the mid-Tertiary date; Deevey assumes the Pleistocene date.

The well-known *Iris* problem (7) is cited, a problem involving the discovery of parents of *Iris versicolor,* i.e., *I. virginica* var. *shrevei,* "ranging from the coastal plain through the northern Appalachians and overlapping the range of *versicolor*" (66) ; and the previously unrecognized *I. setosa* var. *interior* in unglaciated central Alaska. Anderson gives for the range of *I. virginica* var. *shrevei,* "Mississippi Valley and Great Lakes region from southern Minnesota and southern Ontario, southwards to Texas and Alabama"; his map shows few Appalachian stations and no coastal plain stations. According to Deevey, Anderson states "that *versicolor* was synthesized when Pleistocene glaciation mingled the populations of *setosa* var. *interior* and *virginica* var. *Shrevei,* presumably along the margin of the Wisconsin ice sheet in Minnesota and North Dakota". But Anderson states that "*Iris versicolor* is either late pre-glacial or inter-glacial" and that "the present distributions of the species would suggest that the original hybridization (or hybridizations) took place in the interior of the continent, perhaps in the general region of the present-day Great Lakes". Further, he thinks that "very anciently the *Iris virginicae* of the Atlantic seaboard became slightly differentiated from those of the Mississippi Valley", thus carrying the evolutionary pattern well back into Tertiary time. Anderson's statements are based upon "a detailed morphological census" extending from Alabama and Mississippi to northern Michigan.

In discussing the problem of endemism, the necessity of determining the kind of endemics is pointed out. A localization of endemics, even if from several genera, does not necessarily indicate great age. If such endemics are surrounded by related widespread species, they are young. (See certain endemics of the shale barrens.)

More evidently within the province of plant geography is the discussion of "persistence of plant communities on the Schooley peneplane". In the first place the relative values of disjunct oc-

currence of a single species and of disjunct occurrence of a community are discussed. Most plant geographers consider the latter to be more significant (55, 94), but no plant geographer has ever stated or implied that there is any " geometrical progression " involved, or that the occurrence together of ten species of the same community is " n^{10} times as remarkable as the occurrence of one of them ". However, Deevey, in a later paper dealing with marine hydroids (67), says that " one such example of disjunct range might be the result of an accident, either of dispersal or of collecting, and the repetition of the phenomenon merely increases the likelihood that the problem is real ". The question at issue is the occurrence of coastal plain colonies in swamps on the Cumberland Plateau where the old-age topography of the Schooley peneplain still persists, i.e., on undissected remnants of that plain (29, 30). In support of the idea of separate and presumably recent invasion of these swamps by coastal plain species, Deevey outlines briefly the classic principles of " invasion of new habitats " and subsequent succession—the sort of invasion and succession which marks every depression on the young glaciated area. But on the old-age surface of the Schooley peneplain, invasion was not into new habitats. Neither is this a " place where plants of open, dry country, including some grassland species, come largely into question ". A few species do occupy sites comparable to the Pine Barrens; most are in boggy swamps, carpeted with *Sphagnum* and *Pallavicinia,* and none, except the ubiquitous *Andropogon scoparius,* a complex species of many races with distinct range, could possibly be called " grassland species ". This misinterpretation of floristic content of the communities may be at the root of a suggestion, made later in the paper, that " it may have been during the xerothermic interval that the plants moved into the interior ". The complete absence of western species makes this very unlikely. A further misinterpretation of floristic content may in part be responsible for the attempt to line up these relic coastal plain swamps with northern bogs, for the statement is made that the " colony of ten coastal-plain disjuncts on an undissected portion of the Cumberland Plateau is accompanied by northern species, elsewhere rare in the region ". The few somewhat northern species that are present are common and have wide ranges. Unfamiliarity with the terrain is probably responsible in part for the

statement about " the inherent unlikelihood . . . that plants remain on a patch of ground while the ground is uplifted by hundreds of feet and deep valleys are cut all around ".   The " ground " which was uplifted was the entire Schooley peneplain.   As was frequently emphasized, the vegetation of the once low-lying plain became gradually restricted as the area of the plain became smaller; hundreds of square miles still remain, and " deep valleys " are miles away from the larger flats which still harbor coastal plain species.

The comments concerning brief statements on the location of areas of best development and of disjunct occurrences of mixed mesophytic forest climax (32) seem much confused.   For example, the statement is made " (1) that many of the important species and the mixed deciduous forest itself stop at the glacial boundary ".   Against this must be balanced the original statement that " the two most characteristic species of the Mixed Mesophytic forest, *Tilia heterophylla* and *Aesculus octandra,* are abundant to the glacial boundary and into the area of Illinoian glaciation, but have scarcely invaded the area covered by Wisconsin ice ".   Another statement, " (2) that ' the mixed deciduous forest . . . is as rich in species in all layers near (not at) the glacial boundary as it is 200 miles farther south ' " is, in the original, not what is presumably quoted, but " the rugged western margin of the Appalachian Plateau harbors excellent mixed mesophytic forest which is as rich . . .".   Mixed mesophytic and mixed deciduous are far from synonymous, which at once makes the misquotes untrue.   And the stated location, " rugged western border ", introduced factors not present elsewhere.   The fact that the change is near, not at, the glacial border refutes the value of arguments about differences in ecologic factors on the two sides of the boundary; those differences are apparent but are not the causes of the change in forest communities.

Throughout the discussion concerning the idea of persistence (*a*) of coastal plain plants on remnants of a former peneplain, and (*b*) of certain species generally thought of as Tertiary relics of Asiatic relationship in the always unreduced areas, there seems to be confusion about the terms " reduced " (which means reduced to peneplain) and " unreduced " (which means not reduced to peneplain, but always hilly or mountainous).   For note: " the

species believed to have existed on the low-lying Miocene erosion surface [these would be the coastal plain species] . . . ought either to be confined to residuals of that surface [they are] or to have spread out subsequently [some have]; they ought not to *avoid* peneplane remnants [within the whole Appalachian Highland, they do not]. But this is just what some of them do; against *Stuartia malachodendron* [which is on the Coastal Plain and nowhere mentioned in the literature cited] and *S. pentagyna*, American species of an otherwise Japanese genus, confined to Schooley remnants [*S. pentagyna* is confined to always unreduced areas, and is not on Schooley remnants], we may balance *Shortia galacifolia,* confined to a low area at the inner edge of the Piedmont [its occurrence in several places in the always mountainous Blue Ridge province has been discussed under "Extra-Continental Relations"]". That is, *Stewartia pentagyna* and *Shortia galacifolia,* and many other of these ancient species are in the areas never reduced to peneplain.

A final topic under "Southeastern United States during the Pleistocene" is one dealing with the effectiveness of glacial climates south of the drift border. This is best considered in connection with the next section of this review.

Other topics concerning glaciated eastern North America, such as northern relicts and survivals from interglacial ages, have already been included.

It is of interest to see stated in the "Summary", one of the reasons for promulgating the hypothesis of Pleistocene origin of present distributions: "Because the attempt has never been made before, and therefore seemed eminently worth making, there has been an effort in this presentation to look at existing animal and plant distribution as a whole from the standpoint of Pleistocene geography". As a result of this viewpoint, these summary statements concerning the "Southeast" are in order: "If the species have been in their present habitats . . . since early or middle Cenozoic time, it is difficult to understand the obvious fact that Pleistocene climatic changes in the general region were extensive. [See next section for discussion.] That is, the evidence from Pleistocene fossils [in coastal areas] conflicts with the pattern of existing distribution as interpreted by biogeographers". Therefore, "the relicts on peneplane remnants must have been moving

around during glacial ages, some of them perhaps having been driven into Mexico and peninsular Florida ".

This contribution to biogeographic thought will challenge opponents and proponents of the theory to more careful and precise statements of facts on which their beliefs are built.   Further evaluation of the hypothesis is best included with the discussion to follow.

HOW FAR-REACHING WERE THE EFFECTS OF GLACIATION?

In order to evaluate the interpretations made in regard to general distribution patterns and to the many specific cases which have been reviewed, it is necessary to consider the very important question—How far-reaching were the effects of glaciation?   The direct physical effects—deposition of till and outwash, ponding of streams, drainage changes, etc.—are well known.   The effect on climate can only be inferred from evidence at hand, and climate is of great importance in the geography of plants.   Some of the inferences are based on physical features of the land and water, some on Pleistocene fossils, some on cytogenetics, chromosome numbers and introgression, and others on distribution patterns of present-day vegetation.

Bryan (36) believes that an arctic climate must have bordered the ice at each advance; however, he suggests that the zone of periglacial climate may have been very narrow in some places because the plains area in the interior United States allowed a free sweep of southwesterly winds.   The distance beyond the ice sheet to which the glacial anticyclonic winds would be effective would thus be modified.   Where such cold winds were overlain by moisture-bearing winds from a southerly direction, clouds, rain and fog would be produced.   Such effects could be expected if, as Berry (23) believed, it is " probable that the extensive Pleistocene glaciation was due more to unbalanced precipitation than to any great degree of secular change in temperature ".

Raup (155) suggests that boreal land-form studies may be useful in connection with problems of the glacial border.   As the effects of frost action are a function of climate, we should look for " the effects of this climate and its attendant frost action in the soils and topography " both beyond and within the glacial border.

As yet, the study of frost phenomena is in comparative infancy. Recognition of ancient frost forms is often difficult. Various solifluction features, block fields, rock streams, fossil or ancient stone rings and stone stripes have been recognized in temperate latitudes, both within and without the glacial boundary (69, 155, 178–180). Evidence of congeliturbation (of debris produced by frost-riving and moved by solifluction) likewise can be found within and without the glacial boundary. Such features are the result of deep seasonal freeze and thaw. Differences in topography, or the configuration of slopes, such as may be seen at different distances from the drift border, give clues to probable climatic differences of glacial time (69). Where there is evidence of cryoplanation, i.e., the process of molding the landscape by frost action, there must have been fairly severe frost action. The plant geographer is particularly concerned with the question as to how far outside the glacial boundary and at what altitudes features arising from severe frost action occur.

Periglacial frost phenomena (block concentrations, block cascades, etc.) have been described in the eastern part of the Driftless Area at latitude 43° N., within 10–20 miles of the Wisconsin glacial boundary. These are interpreted as indicating that, for at least a part of Wisconsin time, the climate of the Driftless area was more rigorous than at present and had some similarity to that now found in subarctic regions (178). Periglacial block streams have been found along the northern Blue Ridge from southern Pennsylvania to northern West Virginia (latitude 39°– 40°) (179, 180).

It is believed that a " surficial deposit and the associated landscapes in the periglacial area, or area within a few tens of miles of the Wisconsin drift border [on the high Appalachian Plateau of northcentral Pennsylvania] are the result of processes caused by the adjacent Wisconsin ice sheet " (69). Topographic contrasts can be seen in a traverse from the drift border southwestward for about 75 miles (latitude ca. 40°–41°). Near the drift border " the evidence is good that in favorable localities the present frost climate is sufficient to maintain a miniature blockfield or to produce miniature boulder rings if the vegetation is removed " (69). All of these features are said to indicate that frost action in the periglacial belt in northcentral Pennsylvania was more intense than

at present, and that the annual depth of frost penetration was as much as six feet and somewhat greater than at present. It is a known fact that winter temperatures of soil beneath a vegetation cover and of soil not so covered are very different (for data, see 215).

Blockfields and thick surficial deposits occur in the higher parts of the Appalachians as far south as the Great Smoky Mountains (69). In the Great Smoky Mountains frost phenomena give evidence that there was a timber-line, probably in the last cold phase of the Pleistocene, at an elevation between 4000 and 5000 feet (120), which would mean a lowering of altitudinal belts of about 2000 feet. As these mountains rise from elevations of about 1000–1200 feet, there was still ample altitudinal range for the several forest zones now represented on the slopes, and habitats sufficiently similar to permit the necessary downward and upward migrations of species.

Additional physical features which may give some idea of glacial climates are outlined by Flint (87). Of these, evidence of chilling of sea water and of the formation of sea ice are of value in suggesting possible coastal conditions. " Studies indicate that there was general cooling of the water in middle and low latitudes ", the amount of cooling varying from place to place (144). Although the broad features of oceanic circulation were probably similar to the present circulation, there were important differences. Cold water extended farther south than at present, as indicated by the finding of ice-rafted pebbles in the western North Atlantic as far south at latitude 40° N., and " possibly pack ice extended as far south as 40° N. Lat.". This affected the Gulf Stream, and " it is doubtful whether the northern edge of the Gulf Stream system reached a latitude much higher than that of Cape Hatteras " (144). As a result it is probable that coastal areas of eastern United States were colder than at present, at least as far south as North Carolina, and possible that fogs were frequent toward the southern limit of the cold air mass overlying the cold drift.

Pleistocene fossils give good evidence of climatic conditions, provided the plants grew in the area where the deposit is found, and that their physiological requirements and tolerance ranges were the same as those of modern biotypes of the species represented. " Most widespread and common plant species consist of a

large number of genetically different biotypes, many of which differ widely in their ecological preferences. This is . . . the basis of the ecotype concept, which conceives of these widespread species as consisting of several clusters of similar biotypes, each cluster, or ecotype differing from other ecotypes in its ecological preferences " (183). White spruce, black spruce, balsam fir, jack pine, and other common and widespread species are ones commonly emphasized as indicative of climatic conditions in which their ecotypes in the North are now growing. There may have been other ecotypes in the past, just as there have been other species (cf. South Carolina buried soils), and these cannot be identified by plant fragments and pollen grains. It is not suggested that the ecological requirements were greatly different, but they may have been at one extreme of the tolerance range as manifested today.

A few deposits are selected to illustrate possible significance of fossils in Pleistocene deposits.

The Two Creeks forest bed in eastern Wisconsin (211, 212) is of particular interest because it gives evidence of conditions at the edge of an ice sheet, but not one of those which forms part of the glacial boundary. A spruce forest established itself on the lake flats exposed when the waters of the Glenwood stage of Lake Chicago fell to below the present level of Lake Michigan; this was when the Cary ice-front was somewhere north of the Straits of Mackinac. Readvance of the ice (of the Mankato substage) ponded the water throughout the forest, and silt was sifted between the upright moss plants which were buried alive (chloroplasts remain). Then the area was overridden by ice (Mankato) and trees were pushed over. The forest had been thriving for at least 62 years before the gradual decrease in width of growth rings began 20 years before the forest was destroyed. The majority of the logs point in a southwest-northeast direction (the advance of ice was from the northeast), and " one log, seven feet long, was found partly attached to its stump, and leaning at an angle of forty-five degrees . . . . About three feet of sedimentary deposit accumulated before the ice reached the spot. When the ice did override the area it apparently pushed this tree over to an angle of forty-five degrees in the soft mud and sand. Then it tore off the portion which protruded from the sediments leaving a shredded and twisted end to the log. This shredded character of the wood

is indicative of live or very recently killed timber " (212).   Although spruce forest is a northern type, its persistence at the very margin of the ice at latitude 44° N. is significant.   Wilson has found that *Picea* rapidly invaded newly exposed soil, but that this forest zone was only a few miles wide.   It is only reasonable to assume that at lower latitudes the climatic effects of proximity of ice would be somewhat less.

A late Pleistocene deposit in Minneapolis contains the remains of species which grew in a bog forest (larch, black spruce) and in a climax forest (white spruce, fir, white pine, paper birch) at a time when the retreating ice front " was certainly not more than 150 miles distant and probably very much closer " (55).   While the bog forest type still lingers nearby, " the conifer forest which once inhabited the uplands, has been entirely superseded, here and for a hundred miles northward, by oaks, maples and other deciduous trees " (57).   Evidently, forest displacement even at latitude 45° N. was not extreme.

If the plant remains of the Little Bayou Sara deposit in Louisiana—where " the remains of typically northern species " have been found with those of southern species (see " Pleistocene History " and 35)—are of early Sangamon time, as has been suggested (67), they date from a time of waning of the Illinoian ice sheet which had been sending meltwater into the Mississippi River some 600–700 miles to the north (more if all the meanders are included).   Climatic conditions had not been severe enough to displace *Taxodium* (stumps in situ) ; spruce is an early invader of newly exposed soil, and cones floating down the river could have supplied seed.   The uneroded condition of a spruce cone in the deposit is given as evidence that it was not transported any great distance.   Cooler summers than now, with more fogginess which might easily result from the nearness of cold water, may explain the mixture, which does not indicate displacement of the sort of vegetation now prevalent in the latitude.

Some buried soils of Pleistocene age (probably early Pleistocene) near Spartanburg, S. C., contain an interesting assortment of pollens.   A reconstruction of the vegetation of the area during the time of sedimentation would be: " The rolling uplands were covered by a climax of oak-hickory-chestnut ; ravines and protected slopes contained stands of mixed mesophytes ; several places where

small streams were impounded postclimax spruce-fir grew on and around bog-like basins; over the upland the prevailing climax was interrupted by stands of pine and pine-hardwood mixtures " (39). A significant fact is that " the *Abies* is not one of the modern species of Eastern America"; it may be an extinct species. Can it be possible that this is evidence that ancestral fir, and perhaps spruce, had been in the East since the time of the early (Mesozoic) records? As an explanation of the spruce-fir community in the vegetation pattern of the Spartanburg area, the possibility of pronounced frost pockets suggests itself. Near Petersham, Mass., at an elevation of 1100 feet on the Harvard Forest, red spruce occupies a frost pocket where temperatures 22° F. below those of the surrounding deciduous woodland are recorded; on Mt. Monadnock, only 25–30 miles to the north, the spruce zone begins at an elevation of about 2300 feet.

The North Carolina pollen profiles (see Pollen Record) indicating climates during glacial ages and subages considerably cooler than the present, seem to reflect the influence of colder ocean waters and perhaps fog. This pollen evidence of the southward penetration of cooler climate vegetation on the Coastal Plain is in accord with the map showing " the effect of introgression in forming geographic subspecies within *Juniperus virginiana* " ; the northern race extends southward on the Atlantic slope to about South Carolina (9).

How much lowering of temperature was necessary to bring about the various features noted? No estimates are available except those based on lowering of regional snow lines in mountains, where the calculated reduction in mean temperatures range from 4° to 7° or 8° C. in different mountain areas, the highest being for western Europe, Italy and Greece (87). Other statements are comparative only. Reviewing the probable effects of climate on vegetation south of the ice margin, it appears that " the margin of a glacier is held stationary or recedes because wasting equals or exceeds the rate of ice advance " and that " during wasting, surfaces become covered with detritus which . . . may temporarily insulate the frozen mass within ". Thus the marginal band of the glacier would be little different from a perennially frozen soil band in its temperature effects on adjacent areas. Also, atmospheric circulation was affected because of the permanent high-

pressure areas developing over ice-caps; the thermal gradient south of the ice was increased, and hence storminess increased (33).

What were the effects on vegetation? Opinions differ greatly, ranging from those of Deevey who proposed the "hypothesis of Pleistocene origin of existing distribution patterns" and suggested that "the typical temperate species were pushed south of the Rio Grande and deep into peninsular Florida", to those of other authors who maintain that it seems entirely possible that some temperate species may have persisted at or near the ice margin and that displacement amounted to a narrowing of the deciduous forest belt at the north and lowering of its altitudinal range in the mountains. It is doubtful that deciduous forest ever could have occupied any considerable area on the Coastal Plain where soils, except in local areas on river bluffs, are unsuitable. As Cain has suggested (38), "much of the whole region south of the terminal moraine provided territory for preservation, but the centers were generally the regions of varied topography and conditions (the Southern Appalachians and Cumberlands, the Ozark plateau, etc.)".

It must be remembered that glaciation was not a single event, that the hypothesis that temperate species were "pushed" far south must assume that similar migrations took place not once but during each cold phase of the Pleistocene—in Nebraskan, Kansan, Illinoian, and Wisconsin time—with some to and fro movements in the glacial subages. If "the warmth-loving species, including many or perhaps most of the 'Miocene relicts', survived in peninsular Florida and in Mexico, and have subsequently migrated to their present localities", the migrations of Wisconsin and post-Wisconsin time were not the only ones. In other words, these temperate species, whose ranges are so simply explained by an hypothesis of persistence, must have gone to Mexico or Florida at least four times, only to return and assume a pattern of distribution in favorable habitats related to Tertiary physiographic history. Yet no evidence has been left behind in these remote areas, either in the fossil record or in the form of isolated occurrence of temperate species of restricted range; the Mexican occurrence of species of wide range and low rates of evolution, as *Liquidambar styraciflua, Mitchella repens* or the subspecies of

Fagus, is more easily explained by disruption of range because of late Tertiary aridity than by Pleistocene migration. Could any considerable population of mesophytes of rich humus soil find edaphically suitable areas on the Coastal Plain in which to survive while in peninsular Florida, or to occupy while migrating to and from Mexico?

It is suggested that the coastal plain disjuncts on the Appalachian Upland may have taken part in these migrations, " some of them perhaps having been driven into Mexico and peninsular Florida " (66). If these disjuncts arrived by post-Wisconsin migration from Florida and Mexico, or even from the Gulf and South Atlantic Coastal Plain, how can the relationships displayed by *Asclepias, Sarracenia,* etc., be explained? Can such distinct specific differentiation as is apparent between upland and coastal plain species of *Conradina* be ascribed to the last few thousand years? Is it possible that migrations from upland to coastal plain and back again took place four times, each move involving the spanning of wide edaphic barriers?

The edaphic requirements of species could not have changed radically each time that temperatures were lowered, at least not enough to have permitted the many species of exacting requirements (which are the ones of local or restricted distribution) to move hundreds of miles across lands offering few if any suitable habitats. If such migrations took place, they must have been initiated not by low temperatures prevalent at the time of maximum development of an ice sheet, but during the gradual lowering accompanying advance of ice sheets. Yet we know from the evidence of the Two-Creeks forest bed that there a forest stayed until actually overwhelmed by ice. Also, the return migration could not have been delayed until the onset of unfavorable temperatures in the area of refuge, for by that time the intervening area would have been impassable, if it were not always so. Moreover, the temperature tolerance range of most species is considerably more than that to which they are naturally subjected, except at the limits of range. For example, *Shortia galacifolia* is hardy in Quebec and New Hampshire (116); *Rhododendron catawbiense* in northern New York State; *Rhododendron carolinianum* in Norfolk, Connecticut, where hundreds of plants have established themselves from self-sown seed, and during which time a temperature of –27° F. was recorded (89); *Neviusia alabamensis*

shows no effects of temperatures of –13° F; *Magnolia tripetala* can be grown in Minneapolis. These " Miocene relicts " are hardly " warmth-loving ".

Against such an hypothesis of extreme southward migration, of the shaping of distribution patterns by Pleistocene glaciation, and of Pleistocene speciation and subspeciation of most taxa, we must weigh the known stability of many of our tree species and the inferred stability of others (low rate of evolution indicated by close relation of American and Asiatic species), the relative positions of diploid and tetraploid races of some species, the patterns of introgression, the tolerance range (temperature, soil, length of day, etc.), the distribution patterns of a great many species. We must recognize moderate shifts in range, shifts which would permit such xero-mesophytes as the species of *Cercis* to come into contact, shifts which would modify or determine northern limits of range, and of course the several easily demonstrable shifts of late-glacial and postglacial times. We must look for regional, not general, climatic influences which can explain changes in coastal plain vegetation indicated by pollen diagrams. We must keep biotype variability in mind.

The many facts considered under the headings " Floristics " and " Contributing Fields of Botany " must be weighed, along with those derived from known physical effects of glaciation, the fossil record, and physiographic history of unglaciated eastern United States, in arriving at a reasonable interpretation of the intricate but consistent pattern of distribution.

Evidence indicates that in many instances the " historical factors " determine the physiographic area in which a species occurs; the climatic factors of the recent past and the present determine the geographic limits; the edaphic factors determine the precise area occupied within the limits of the larger areas determined by past events and present and past climates.

ACKNOWLEDGMENTS

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THE BOTANICAL REVIEW

FUNGI THAT ATTACK MICROSCOPIC ANIMALS [1]

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INTRODUCTION

The term " predacious fungus " is usually applied to those micro-fungi that capture, kill and consume microscopic animals. Research during the last two decades has shown that this unusual mode of life is far from being uncommon, since the predacious fungi are to be found with great regularity in leaf-mould, rotting wood, soil, dung and decaying plant material of many kinds. In spite of their common occurrence and apparently world-wide distribution, however, they have attracted but little attention from botanists in general, and are scarcely more familiar to many students of fungi.

The means adopted by these fungi for capturing their prey are varied, but the most usual adaptation to the predacious life is the production of a sticky substance, by means of which an animal coming into contact with the mycelium of the fungus is held, as a bird is caught by bird-lime. In addition to the possession of this

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[1] Some of the material contained here has been used in a thesis for the degree of Ph.D. in the University of London.

sticky fluid, there may or may not be structural modification of the mycelium to assist in the capture of prey. Mechanical traps, working on the principle of the rabbit snare, are also common. The animals captured are usually Protozoa or nematode worms, though several fungi are known to attack rotifers, and one species, *Arthrobotrys entomopaga,* has been observed (54) to capture springtails.

In addition to the actively predacious species which trap living prey, many fungi are known which live as internal parasites in amoebae, nematodes and other small animals, often causing severe epizoötics in Petri dish cultures. Most of these fungi have spores that stick to the exterior of the host animal on contact and germinate to produce an endozoic mycelium. These parasites, though not actively predacious, are usually classed with the predacious fungi, and an absolute distinction between internally parasitic and truly predacious habits is not always an easy one to draw, as may be seen, for example, in the genus *Nematoctonus.* Probably those species which have adhesive spores are best regarded as being predacious during their reproductive stage, the more so as their spores are often presented in such a way as to ensure the maximum probability of their being accidentally picked up by a passing animal.

HISTORICAL OUTLINE

The earliest record of a predacious fungus is the description of *Harposporium anguillulae* as long ago as 1874 (107). It was not until some 14 years later that Zopf, in a classical paper, recorded the first observation of the capture of living nematodes by *Arthrobotrys oligospora,* one of the commonest of all the predacious fungi (131). This fungus was first described as a saprophyte in 1852, but its predacious habit was unsuspected by its discoverer (84). Nearly 20 years later it was observed (129) that germinating spores of *A. oligospora* often produced a mycelium in which curving, anastomosing hyphae formed a complex system of loops, but the significance of this phenomenon was not realised. Zopf grew the fungus in Geissler chambers in company with nematodes, and was able to demonstrate that eelworms were caught by the loops, and that, after the death of the animal, which took place in from two to two and a half hours after capture, the fungus intruded a system of absorptive hyphae into the body of the nematode and

consumed its contents. Zopf regarded the capture of the nematode as the result of purely mechanical entanglement in the loops, which he thought to be elastic; the fact that a sticky substance was secreted was not recorded until later (40).

The history of *A. oligospora* is paralleled by that of *Dactylella ellipsospora*. This fungus was first described in 1851 as *Menispora ellipsospora*, and later transferred to the genus *Dactylella* after it had again been found growing on rotten wood near Birmingham, England (80). Fifty years later in America, Drechsler (40) demonstrated that a fungus whose conidia resembled those of *D. ellipsospora* was able to capture nematodes by means of adhesive knobs which were borne laterally on short stalks at frequent intervals along the hyphae. It is interesting to record that a fungus bearing similar knobs was recorded in 1888 by Zopf (131), but he did not see the conidia, and thought that the stalked knobs were spores.

The next discovery of importance was *Zoophagus insidians*, an aquatic Phycomycete which captures rotifers (125). This interesting fungus has since been observed by other workers in Britain (4) and elsewhere. The systematic position of *Z. insidians* is open to doubt. The earlier workers described sexual organs which appeared to place it in the Oomycetes, but there appears to be some possibility that there was confusion with another fungus, and it has been suggested (55) that *Z. insidians* might be better placed in the Zoopagaceae, a family of the Zygomycetes.

Some early records from France (116) are of historical interest. Parasites of amoebae were described and placed by their author, probably incorrectly, in the Saprolegniaceae. From the published descriptions and drawings it seems possible that we have here a very early record of the Zoopagaceae, for some of the structures figured and described are suggestive of *Endocochlus or Cochlonema*.

What might well be termed the modern era of the study of predacious fungi began in America in 1933 when Drechsler, in four short papers (27–30), announced the discovery of several entirely new kinds of predacious activity. This was followed by a long series of descriptions of new predacious species. His first communications were mainly concerned with the Zoopagaceae, a family consisting entirely of obligate predators, mostly attacking amoebae

in decomposing vegetable matter. In 1937 he published a long paper (40) dealing with the predacious hyphomycetes, in which, besides giving details of the predacious activity of *Arthrobotrys oligospora, A. superba, Dactylaria candida* and *Dactylella ellipsospora,* he described a number of new species belonging to the same predacious series. Since that time the predacious fungi have been particularly associated with his name, and the monumental store of information that he has unearthed and is continuing to uncover will stand as one of the classic researches of mycology.

In addition to the work of Drechsler, no historical account of the predacious fungi would be complete without reference to the interesting contributions which have recently come from France, particularly in the spheres of physiology and the possible use of predacious hyphomycetes for the biological control of nematodes parasitic in plants and animals. Reference to this work will be made later.

SCOPE OF THE PRESENT WORK

In a review of even so limited a field as that presented by the predacious fungi, a certain amount of selection is inevitable if the work is to be kept within reasonable length. In the present contribution consideration is given only to the two main groups of predacious fungi, namely, the Zoopagaceae and the predacious hyphomycetes, together with a few other forms which are included on account of their similar mode of life or because they are intrinsically interesting. No mention is made of the entomogenous fungi, with which the name of T. Petch will always be associated, nor of the various species of Chytridiales that have from time to time been described as parasitic on animals. Fungi parasitic on eggs of animals or on nematode cysts are not included, and species of doubtful validity are ignored.

In describing the predacious fungi, it will be convenient to consider them under four heads—the Zoopagaceae, the Arthrobotrys [2] series of predacious hyphomycetes, the endozoic predacious hyphomycetes, and other forms. In group four are included three aquatic species of doubtful systematic position, and some endozoic parasites mostly belonging to the Lagenidiales: the former because

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[2] It must be understood that the use of this term here is one of convenience only, and that no taxonomic or phylogenetic implications are intended.

of the possible relationship of two of them with the Zoopagaceae, and the latter as examples of fungi outside the main predacious series that have adopted this unusual mode of life.

SYSTEMATIC REVIEW OF THE PREDACIOUS FUNGI

ZOOPAGACEAE.   The Zoopagaceae are a family of Zygomycetes consisting entirely of predacious species, defined by Drechsler in 1938 (42).   Most of them attack terricolous amoebae, but other hosts are recorded, and there are a few species, such as *Stylopage hadra,* that are sufficiently robust to capture nematodes.   Their relationships are obscure; they have been included, not very comfortably, in the Entomophthorales by some authors and in the Mucorales by others; there is little doubt, however, that they should be given ordinal rank, and this has already been done by one author (5).   Apart from their exclusively predacious habit, one feature that sets them apart from most other Zygomycetes is that their asexual spores appear to be true conidia and are not violently discharged.   The conidia may be carried on relatively long aerial conidiophores, or nearly sessile on short sterigmata; they may be single, several along the length of the conidiophore, in groups or in chains.   No indication of a double wall is observable under the most rigorous microscopical observation, nor does their mode of development suggest that they may be modified one-spored sporangioles; if they have been derived from some mucoralean ancestor with elongated sporangia, as are found in the Piptocephalidaceae, they have advanced so far along the evolutionary road that all trace of their origin has been lost.

Two forms of predacious activity are found in the family.   In some, for example, *Cochlonema* and *Endocochlus,* the mycelium is thalloid and internally parasitic within the protozoan host, while in others (*Stylopage, Acaulopage* etc.) a well-developed filamentous mycelium is present, the prey being apparently captured by adhesion and its contents absorbed by a haustorial system of lateral branches.   The genus *Bdellospora* is an interesting intermediate form, the thallus being developed outside the host amoeba by swelling of the infecting conidium, while nourishment is drawn from the host by means of haustoria as in the mycelial genera.

The family at present contains nine genera and 65 species, and has a wide distribution, members having been recorded from Eu-

rope, North America and Australia. There is little doubt that many more species await discovery.

The endozoic habit in the Zoopagaceae is well illustrated by the genus *Cochlonema*. In *C. verrucosum* (32, 72) infection of an amoeba is initiated by one of the fusiform conidia of the fungus becoming attached to the ectoplasm of the animal. A very fine germ tube is put out which penetrates into the endoplasm and gives rise at its apex to a globular swelling. This swelling becomes detached from the germ tube which, with the empty conidium, is cast away by the animal. The globular mass remaining in the animal swells, and from being subspherical it elongates to become sausage-shaped. As growth continues, it bends sharply over on itself and becomes coiled in a close spiral of about one and a half turns. In a mature thallus the diameter of an individual " hypha " is about six microns. As the fungus grows, the endoplasm of the amoeba is progressively absorbed.

During early stages of infection the amoeba continues to move about, ingesting food material and seeming little if at all the worse for the presence of the fungus. Multiple infection by more than one conidium is not uncommon, and living amoebae may be seen, each with several thalli at different stages of development, feeding on its endoplasm. Eventually, however, the effects of the fungus make themselves felt; as the endoplasm of the amoeba becomes more and more depleted, the animal becomes increasingly sluggish, finally assuming a more or less rounded shape and ceasing to move at all. The fungus continues to feed on the dead or moribund host until nothing but the shrivelled remains of the ectoplasm is left.

Reproduction usually begins when much of the endoplasm of the host has been consumed and the animal is practically, if not quite, dead. From various points on the coiled thallus delicate fertile hyphae grow out through the ectoplasm of the host and, turning upwards, rise vertically into the air. They become constricted at intervals and form chains of spindle-shaped conidia, 30 or more to a chain. When mature, the chains are easily disrupted, the individual conidia then being strewn about the surface of the substratum in large numbers where they can be picked up casually by passing amoebae, so that it is hardly surprising that in Petri dish cultures severe epizoötics among the amoebae may result.

Sexual reproduction occurs in the manner usual among Zygomy-

cetes. Slender outgrowths from the thalli emerge from the remains of the host, bearing club-shaped gametangia at their ends; the junction between suspensor and gametangium is often marked by an abrupt knee-shaped bend. After fusion of the gametangia, a zygospore develops in the usual way.

Various other species of *Cochlonema* have been described (32, 39, 43, 44, 47, 49, 55, 57, 70) from America, differing in size and shape of the thalli and spores. Most of them attack amoebae, but a few are parasitic in other Protozoa.

The genus *Endocochlus* resembles *Cochlonema* in habit, and is also parasitic in Protozoa. It is distinguished by the conidia being borne singly, erect and practically sessile, as lateral outgrowths from prostrate fertile hyphae. Four species have been described, all from America (32, 37, 65).

An interesting intermediate stage between internal parasitism and the strictly predacious habit is seen in *Bdellospora helicoides* (32). The conidia in this monotypic genus are spindle-shaped and formed in erect chains as in *Cochlonema*. A conidium adheres to the exterior of an amoeba and intrudes a haustorium into its endoplasm. Instead of an endozoic thallus being formed, the conidium itself grows as nutriment is absorbed from the host, and develops into a lemon-shaped swollen body which is carried about by the amoeba until exhaustion of the endoplasm makes further movement impossible. At maturity, after the host has succumbed to the parasite, chains of conidia are formed, thus spreading the fungus among the population of amoebae. Sexual reproduction takes place by fusion of gametangia, the suspensors coiling tightly round one another. This unusual fungus has so far been recorded only in America.

Recently (70) some rather unusual zoopagaceous parasites of amoebae have been described from America. In *Aplectosoma* the endozoic thallus is cushion-shaped, and the conidia are formed in chains as in *Cochlonema*. Another unnamed amoeba parasite has a U-shaped thallus which bears spore-like bodies projecting to the exterior through the ectoplasm of the host. The relationship of these curious fungi to the rest of the Zoopagaceae is obscure, though it can hardly be doubted that they must be placed in that family.

As an example of the strictly predacious series of Zoopagaceae,

Stylopage rhynchospora may be quoted. This rather common fungus has been reported from America (44) and England (75). Instead of an endozoic thallus, we have here a well-developed mycelium of delicate non-septate hyphae which branch sparingly. Amoebae coming into contact with the mycelium stick to it, possibly on account of some adhesive substance secreted by the fungus. The ectoplasm of the amoeba is penetrated by a system of fine haustorial branches which originate at a point on the hypha in contact with the animal and spread throughout the endoplasm like the branches of a bush. By this means the fungus gradually absorbs the contents of its prey, so that eventually only the shrivelled remains of the ectoplasm remain attached to the mycelium. During the initial stages of attack the amoeba appears to be little harmed, as cytoplasmic streamings continue and the contractile vacuole functions normally. With further development of the haustoria inside it, however, the animal assumes a rounded shape, all movements cease and, with progressive absorption of the endoplasm, death supervenes.

The conidia of *S. rhynchospora* are borne singly at the apices of tall erect conidiophores. The spores are ovoid with a bluntly rounded beak at the distal end; this beak may be devoid of cytoplasm and may carry a certain amount of sticky fluid which sometimes causes conidia lying on the substratum to adhere together tip to tip. Sexual reproduction occurs by fusion of slender gametangia, and the resulting zygospore has a thick wall which, as is usual in the family, is ornamented with hemispherical warty protuberances.

A number of other species of *Stylopage* have been described (33, 34, 36, 37, 42, 44, 55, 62, 64, 81). Most of them capture Protozoa, but two species are large enough to prey on nematodes. *Stylopage hadra* (34) has a branched mycelium with hyphae about five microns wide. On contact with a wandering nematode, an intensely stickly fluid is secreted which holds the eelworm fast, in spite of its desperate struggles to get away. The chemical nature of this adhesive substance is unknown; it appears to be formed only on contact with a nematode and is extremely efficient, for, although the animal may pull the mycelium that holds it violently from side to side during its struggles, it is unable to escape once it is fairly held. When the prey has become quiescent, either from exhaustion or from some unknown other cause, a

bulbous swelling is formed on the fungal hypha at the point of contact. This swelling appears to act as an appressorium, and from it an outgrowth penetrates the integument of the nematode and becomes a starting point from which trophic hyphae ramify throughout the carcass of the animal and absorb its body contents. In the end, only the integument of the eelworm is left, and the protoplasm of the trophic hyphae is resorbed by the parent mycelium. *Stylopage leiohypha* captures nematodes in a similar manner; it differs from *S. hadra* in its smaller conidia and in the absence of the bulbous appressorium (36). Other members of the Zoopagaceae which capture eelworms in a like manner are *Cystopage lateralis* (47, 73) and *C. intercalaris* (55), in both of which the only known form of reproduction is by means of chlamydospores which are lateral in the first species and inter-calary in the second. The curious species *Euryancale sacciospora* (44), internally parasitic in nematodes, is also worthy of mention here. Another unnamed species of *Euryancale* has recently been recorded by Drechsler (70).

The two remaining genera of Zoopagaceae are predacious on amoebae and other Protozoa, capturing their prey by adhesion to the mycelium. They differ from *Stylopage* in their habit of sporu-lation. In *Acaulopage* the conidia are borne singly at intervals along the hyphae, standing vertically on short sterigmata. A notable feature of this genus is the strong tendency for evacuation of cytoplasm from the distal end of the spore, leaving an empty appendage. Often the appendages are multiple; in *A. tetraceros* (32) the spore is shaped like an inverted cone, with from three to six filamentous appendages arising from its flattened distal end, while in *A. acanthospora* and related species the whole distal half of the spore is covered with short spiny appendages. The sig-nificance of these structures, if any, is unknown, but it is of some interest to note that several species of *Acaulopage* have been ob-served in aquatic or semi-aquatic habitats (113, 114), and it is not impossible that the appendages may be connected with floatation. A comparison is suggested with some of the aquatic hyphomycetes described by Ingold (89–93), though these do not appear to be predacious. Eighteen species of *Acaulopage* have been recorded, occurring in England (75, 77, 113, 114) and in America (33, 37, 42, 43, 47, 49, 55, 57, 62, 64).

Zoopage, the type genus of the family, also captures Protozoa,

principally amoebae. In this genus the conidia are elongated and formed in long erect chains attached basally to short sterigmata. The mode of predacious activity is similar to that in *Stylopage* and *Acaulopage*. The species of *Zoopage* are often difficult to identify, as the spore measurements and other diagnostic characters tend to vary slightly (77) ; it may be that the genus is somewhat labile and that a splitting of some of the species into varieties may become necessary in the future. The genus contains ten species (32, 37, 39, 42, 63).

Taken as a whole, the Zoopagaceae appear to form a compact and closely interrelated family. Their strictly predacious mode of life, the means adopted to snare their prey, their conidia and their very characteristic zygospores seem to mark them off sharply from the Mucorales, on the one hand, and the Entomophthorales, on the other, as a well-delimited group of Zygomycetes.

ARTHROBOTRYS SERIES OF PREDACIOUS HYPHOMYCETES. This is a group of genera belonging to the family Moniliaceae of the Fungi Imperfecti. Most of them attack nematodes and show various structural and physiological modifications to enable them to capture their living prey. These organs of capture may be classified into a number of types:

Adhesive Networks or Branches. In this type of mechanism, short lateral branches from the mycelium curl round and anastomose either with similar branches or with the parent hyphae, thus forming hyphal loops. From these, other loops arise, forming eventually complex systems of networks in three dimensions. Eelworms are captured by adhesion to the loops through the agency of a sticky secretion, and capture may be assisted by entanglement. This type of mechanism is found in *Arthrobotrys oligospora* (40), *Dactylella reticulata* (114), *Dactylaria thaumasia* (40), *Trichothecium flagrans* (74) and many others. Sometimes the networks are relatively simple, as in *Arthrobotrys musiformis* (40) ; the adhesive apparatus may consist of short branches which only occasionally fuse to form networks, as in *Dactylella cionopaga* (67), or of irregular lobed outgrowths from the mycelium, as in *Dactylella lobata* (79). In *D. gephyropaga* the networks are scalariform (40).

Adhesive Stalked Knobs. The predacious apparatus consists of a subspherical knob, borne on a short lateral branch from the

mycelium; the stalk is usually composed of one or two cells only, as in *Dactylella ellipsospora* (40) and *D. mammillata* (26). Nematodes are captured by adhesion to the knobs.

Non-Constricting Rings. Three curved cells join up to form a closed ring at the end of a short branch. A nematode accidentally passes its head into the ring in the course of its wanderings, and in attempting to force its way through, it becomes firmly wedged and is unable to get clear. No sticky substance or mechanical closure of the ring appears to be involved in this device. Usually non-constricting rings are accompanied by adhesive knobs, as in *Dactylaria candida* (40).

Constricting Rings. The constricting ring is built up of three curved cells, as in the previous mechanism, but here capture of the nematode is not passive. When a nematode pushes its head into the ring, the three cells suddenly enlarge to more than double their former diameter, at the same time shortening somewhat; the result of this is that the opening of the ring is practically obliterated and the nematode is held fast by constriction. The stimulus that operates this remarkable trap appears to be the friction set up by the nematode on the inner surfaces of the cells of the ring. Constricting rings are found in a number of species, for instance, *Arthrobotrys dactyloides* (40), *Dactylella bembicodes* (40), *Dactylaria gracilis* (77) and *Trichothecium polybrochum* (40).

Whatever the trapping mechanism, the ultimate fate of the prey is the same. When the animal is dead or moribund, its integument is penetrated by an outgrowth from the fungus, from which trophic hyphae grow and ramify throughout the carcass of the prey, absorbing its contents. Under favourable conditions, nematodes may be captured in very large numbers, especially by those fungi that employ the sticky network mechanism.

Unlike the Zoopagaceae, which appear to be obligate predators, members of the *Arthrobotrys* series can easily be isolated in pure culture, and grow well on most of the usual laboratory media.

To illustrate the working of adhesive networks, *Arthrobotrys oligospora,* the best-known of all the predacious fungi, may be chosen as a typical example. The mycelium consists of branched, septate hyphae which, in Petri dish cultures, spread in radiating lines over the surface of the medium. If nematodes are present in the culture, networks are formed freely, mostly on the surface

of the medium, though they may sometimes be submerged. A network is initiated by a short lateral branch curling back so that its tip comes into contact with its parent hypha a short distance away from its point of origin. Anastomosis occurs between the tip of the branch and the main hypha, forming a loop. Other loops are formed in a similar manner, on or near the original one, eventually forming complex networks, sometimes containing a dozen or more meshes. The hyphal elements forming the loops are noticeably wider than the subtending hyphae, and are also distinctly broader in the middle than at their extremities where they anastomose with other loops or with the main mycelium; in this respect they resemble the cells of the non-constricting and constricting rings, though whether this fact has any evolutionary significance, or whether it is purely functional, is hard to say.

A notable feature of the networks, and one that is very striking when viewed in situ under the microscope, is that the individual loops tend to be oriented in planes at right angles to one another. Some of the loops lie flat on the substratum on which the fungus is growing, while others stand erect like croquet hoops. The general effect is reminiscent of the semi-circular canals of the mammalian ear, and it is probable that this positioning increases their efficiency, for a nematode stuck to one loop may easily become entangled in others in the course of its efforts to free itself. The cells of the loops contain dense cytoplasm and a number of large vacuoles; they often stain rather deeply with haematoxylin or chlorazol black.

The sticky material that holds the prey appears to be secreted by the cells of the loops on contact with the nematode. Soon after capture, a quantity of viscous fluid can be seen in the region of the point of contact, and it seems clear that it is this fluid that is holding the animal. The action of the fluid is extremely efficient; although eelworms are active animals, and specimens more than half a millimetre long may be captured, they seldom escape, and the efficacy of the mechanism does not appear to be adversely affected by moisture.

Death of the nematode commonly occurs two hours or so after capture. The precise cause of death is somewhat in doubt; it is possible, though unlikely, that the animal may succumb to ex-

haustion after its violent struggling to escape. Production of a toxin by the fungus can not be discounted, though there is no evidence whatsoever in support of this. The theory that the animal is killed mechanically by intrusion of an outgrowth from the fungus (40) has, in my opinion, little to recommend it; although such an outgrowth is invariably formed, it usually does not appear until the animal is moribund. Further research on this point is badly needed.

When the nematode is dead or dying, its integument is penetrated by a short branch from the fungus, formed at the point at which the prey is held. Within the animal this branch swells to form a globose structure, the infection bulb, which may be anything from one half the diameter of the nematode upwards; where well developed, the bulb may completely span the animal's internal diameter. From this there grow out trophic hyphae which spread from the bulb in both directions and eventually fill the body of the eelworm. These trophic hyphae are septate, and at first they are filled with cytoplasm. They absorb the body contents of the eelworm, passing the food material so obtained back to the parent mycelium; as this work nears completion they become progressively emptied of protoplasm. Eventually only the integument of the eelworm remains, filled with the now empty trophic hyphae.

Arthrobotrys oligospora reproduces by means of two-celled pyriform conidia which are formed in " heads " at the apices of erect conidiophores. In older cultures the conidia may be in discrete whorls formed successively down the conidiophore; this tendency to nodal arrangement of the conidia is particularly noticeable in pure culture, where a single conidiophore may bear more than a dozen whorls of spores. The conidia themselves are carried on very short sterigmata. Each conidium is divided into two cells which are usually of unequal size, the distal cell being the larger, and there is usually a distinct " waist " between the cells. On germination the germ tube usually arises from the smaller proximal cell. The amount of sporulation varies according to conditions and is usually preceded by an initial feeding period, during which the young mycelium gorges itself on eelworms. Different isolates appear to vary in their intensity of sporulation and also in their aggressiveness towards nematodes; this is a phenomenon which calls for further investigation.

Arthrobotrys superba (9, 40) and *A. conoides* (40, 77) both resemble *A. oligospora* closely, differing mainly in the size and shape of their spores. The conidia of *A. conoides* are similar in shape to those of *A. oligospora,* differing in their greater length, while in *A. superba* the spores are smaller and straighter-sided. In both these species the tendency to nodal development of conidia is strongly marked. In *A. cladoles* (40), *A. cladodes* var. *macroides* (53) and *A. robusta* (80) a different habit of sporulation is found. Instead of the conidia being formed in whorls down the conidiophore, the fertile hyphae themselves are branched, a single head of conidia being formed at the apex of each branch. These three species all capture nematodes by means of adhesive networks, as in *A. oligospora.*

Arthrobotrys musiformis (40, 75) differs from the foregoing species in the relative simplicity of its traps. Instead of complex three-dimensional networks being formed, the traps often consist of single loops, and it is not uncommon to find a loop in the form of a ring composed of four cells. This arrangement is reminiscent of the non-constricting and constricting rings formed by other predacious hyphomycetes, except that the number of cells in the ring is one greater. Similar structures are sometimes formed by proliferation from the adhesive knobs in *Dactylella ellipsospora,* and it is tempting to speculate on a possible evolutionary connection between the condition in *D. ellipsospora* and the three-dimensional networks, on the one hand, and the non-constricting and constricting rings, on the other.

In *Arthrobotrys musiformis* the conidia are large, two-celled and somewhat curved. They are formed in a loosely capitate arrangement at the apex of an erect conidiophore, and in their general appearance are more suggestive of the genus *Dactylaria* than of *Arthrobotrys.* This approach to *Dactylaria* is even more pronounced in *Arthrobotrys dactyloides,* a species that captures nematodes by means of constricting rings.

The adhesive network is found in all the four principal genera of the *Arthrobotrys* series, and, if agar cultures are accepted as a criterion, it is probably the most efficient type of predacious apparatus. In an active culture the heaps of dead and dying eelworms captured by the fungus may be visible to the naked eye, and under the microscope they may completely obscure the traps

that have caught them. Among genera having highly efficient networks may be mentioned *Dactylaria scaphoides* (115), *D. thaumasia* (40), *D. psychrophila* (53), *Dactylella reticulata* (114) and *Trichothecium flagrans* (74).

A different form of network is observed in *Dactylella gephyropaga* (40). Short lateral branches from the hyphae grow out at right angles, at approximately equal intervals. The tips of these branches are then connected to form scalariform networks in one plane. This species has so far been reported only from America.

Clearly related to the network is the type of trapping device that takes the form of adhesive branches. In *Dactylella cionopaga* (67, 75) short branches, usually one, two or three cells long, stand out at right angles to the hyphae that subtend them. These branches are sticky and serve as an efficient means for the capture of nematodes. Sometimes the branches curve over and anastomose to form loops, but the complex three-dimensional type of network is seldom formed. In young cultures *D. cionopaga* can easily be recognised by the spiky appearance of the hyphae with the branches in the one-celled stage. *D. cionopaga* appears to be a relatively common predacious fungus, both in America and England. It has also been observed several times in Denmark by Shepherd.

In *Dactylella lobata* (79) the predacious apparatus consists of one-celled lobes projecting from the hyphae at right angles. In the one-celled condition these lobes, which are subspherical to ovoid, recall the adhesive knob type of trap without the stalk, but they are subject to proliferation, similar lobes growing out from them to form a moniliform branch. By anastomosis simple networks may even be formed. The resemblance of this arrangement to the adhesive branches of *D. cionopaga* is manifest, and it also suggests comparison with the stalked knobs found, for instance, in *D. ellipsospora;* these resemblances may have some evolutionary significance, but the danger of drawing conclusions from evidence of this sort can not be too strongly emphasised. Nothing is at present known about the phylogeny of the predacious fungi, and such resemblances as have been pointed out above may well be homoplastic.

The stalked adhesive knob is known only in the genera *Dactylaria* and *Dactylella.* In *Dactylella ellipsospora* the knobs are sub-

spherical, slightly longer than they are broad, and attached to the mycelium by short stalks consisting of one or, more commonly, two cells. The knobs are formed at fairly regular intervals along the hyphae, and they are often arranged with the stalk standing vertically so that the knob is slightly raised above the surface of the substratum; this position probably assists the capture of surface-moving eelworms. On coming into contact with the knob, the nematode is held by a sticky substance, and in struggling to get away it often comes into contact with one or more other knobs and so is held more securely. When the animal has become quiescent, an outgrowth from the knob penetrates its integument and gives rise within it to a globular infection bulb, as previously described for *Arthrobotrys oligospora,* and from this bulb trophic hyphae grow out in the usual manner and absorb the contents of the eelworm. *Dactylella ellipsospora* reproduces by means of conidia which are formed singly at the apices of erect conidiophores; as in most species of *Dactylella,* the spores are diamond-shaped and multi-cellular, one of the central cells being very much larger than the rest.

Occasionally the adhesive knobs of *D. ellipsospora* show proliferation. From the knob a branch grows out which, curling round, rejoins with the knob, forming a loop of usually about four cells. The loops so formed are not unlike those of *Arthrobotrys musiformis.* Different strains of *D. ellipsospora* appear to vary in the strength of this tendency to proliferate, and in one strain that has recently come to my notice proliferation is the rule rather than the exception. At first sight, under the low power of the microscope, this proliferating strain could easily be mistaken for *Arthrobotrys musiformis.*

The stalked knob trap shows great uniformity among those species that possess it, differing only slightly in size and in the length of the stalk. *Dactylella mammillata* (26) differs from *D. ellipsospora* only in the shape of the conidia, with their pronounced mammillate tips. In *D. asthenopaga* the knobs are slightly smaller, and the conidia are fusiform, with the cells more or less all the same size; this delicate species captures rather smaller eelworms than the two foregoing.

Of the fungi that capture nematodes with the aid of non-constricting rings, *Dactylaria candida* (40) is the best known. The mycelium of septate hyphae bears stalked adhesive knobs in ad-

dition to the rings. Each ring is composed of three cells which are curved in such a way as to close up and form, by anastomosis, a ring. Where the tip of the (morphologically) distal cell joins the proximal one, the two cells are together fused with the stalk; this latter consists usually of two or three cells and is commonly somewhat longer and more slender than the stalk of the constricting type of ring described below.

The non-constricting ring appears to work purely by passive ensnarement. If a nematode casually pushes its head into the opening, the efforts of the animal to push its way through result in its becoming firmly wedged, since the internal diameter of the ring is somewhat less than that of the eelworm. There is no actual swelling or constricting of the ring, nor does any adhesive substance appear to be involved. Once caught, the eelworm is firmly held. As it struggles to free itself it not infrequently happens that the ring is torn away, and the eelworm escapes, still encircled. This may happen more than once, and in a flourishing agar culture of *D. candida* one may see eelworms moving about actively, wearing several rings as an indication of a number of escapes from capture. Such an escape is, however, only of short duration. Even from the detached ring, an outgrowth soon penetrates the integument of the unfortunate animal and, after it has been killed or rendered helpless, hyphae grow out from the cells of the ring and fill its body, eventually absorbing its contents. If the ring is still attached to the mycelium the material absorbed is passed back to the hypha that subtends the ring; where, however, an eelworm has been killed by a detached ring, a new mycelium grows out from its carcass, the ring thus serving as a means of vegetative reproduction. This phenomenon caused one observer (124) to mistake the rings of *D. candida* or a similar species for conidia, and to name the fungus *Annulosporium nematogenum.*

Hyphomycetes with non-constricting rings are usually provided also with stalked adhesive knobs, and there is some variation among the different species in the relative importance of the rings and knobs in the capture of prey. Thus on agar in Petri dish cultures *Dactylaria candida* captures most of its victims by means of the rings, the stalked knobs being seldom effective (40). This tendency is even more marked in *Dactylella leptospora* (40), where adhesive knobs may be formed on germinating conidia. *Dactylella lysipaga* also bears knobs that are sledom used in agar

cultures, most of the work of capturing nematodes being performed by the non-constricting rings with which this species is also provided (40). It must be pointed out, however, that we do not know whether this applies to the fungus growing in its natural habitat where totally different conditions may prevail. It is very dangerous to draw conclusions from agar cultures about the behaviour of fungi under natural conditions.

Of all the means by which predacious hyphomycetes capture their prey, the constricting ring has aroused the widest interest. This remarkable device was first fully described in 1937 by Drechsler (40) for *Dactylella bembicodes* and related forms. In *D. bembicodes* the rings are formed at intervals along the hyphae, each ring being carried on a short, stout, two-celled stalk. Initially the ring appears as a lateral branch which, as it grows out from the main hypha, curls round so that the distal end is brought into contact with the lower part. Anastomosis then takes place, the curved portion forming the ring and the lower part the stalk. When fully formed the ring consists of three curved cells, each of which is wider in the centre than at the ends; the outer side of each cell forms the arc of a circle, while the inner edge is nearly straight, so that while the profile of the ring is circular, the central opening is roughly in the form of a triangle. The stalk usually has two cells, the distal one of which is fused with two of the ring cells. The cells of the ring are somewhat thicker, and the stalk shorter, than in the non-constricting type of ring.

When *D. bembicodes* is growing on agar in the presence of nematodes, the rings are usually orientated perpendicularly to the surface of the medium, either just above or, very commonly, just below it. The rings are thus placed like rabbit snares so that wandering nematodes may readily pass their heads into them. When this happens the three cells of the ring quickly expand to more than twice their original diameters, gripping the nematode and severely constricting it beyond any hope of escape. The stimulus that produces the reaction appears to be a contact one due to the friction of the eelworm's body on the inner surfaces of the ring cells, for it has been shown (8) that rubbing the inside of the ring with a very fine glass micromanipulator needle produces a like result. The time taken for the cells to expand fully, once the reaction begins, is a matter of only a fraction of a second.

When an eelworm has been captured it struggles violently for a time and, since the rings are set fairly close together, it not uncommonly thrusts its tail into another trap and thus is doubly held. After a time it becomes quiescent, probably either through exhaustion or mechanical damage, and is then invaded by trophic hyphae which grow out of the cells of the ring and, penetrating the integument of the animal, extend throughout its body. Absorption of the body contents follows in the usual way. When the substance of the victim has been completely absorbed the trophic hyphae also lose their protoplasm.

The constricting ring trap is found in all the four principal genera of the Arthrobotrys series, and in most instances is remarkably uniform in structure. In *Arthrobotrys dactyloides, Dactylaria brochopage, D. gracilis, Trichothecium polybrochum* and a number of other species the rings follow closely the pattern of those in *Dactylella bembicodes*. Sometimes minor modifications of structure occur; thus in *Dactylella doedycoides* (45) there is a small median projection on the inner face of each cell of the ring, and this species also differs from most in having a slightly swollen tip to its conidiophore, though these features appear to be absent in at least one English strain (26). This median protrusion of the ring cells is to be noted also in *Dactylella heterospora* (51) and *D. acrochaeta* (71). A curious modification prevails in *D. coelobrocha* (61), where, owing to the peculiar formation of the ring, the captured nematode is held by two only of the swollen ring cells.

A much simpler organization is found in *Tridentaria implicans* which has been recorded as capturing nematodes already weakened by an internal parasite of unknown nature (45). The eelworms appear to stick to the tips of undifferentiated hyphal branches which, after capture is effected, often continue to grow, winding round the body of the captive as they do so. This species appears to be only weakly predacious, as is indicated by its habit of attacking eelworms that are already parasitised by another organism. *Trisporina aphanopaga* also captures nematodes by means of undifferentiated hyphal branches which are probably adhesive, though the presence of a sticky secretion does not appear to have been demonstrated with certainty (40).

Tridentaria carnivora, which captures the testaceous rhizopod

Difflugia constricta, is one of the few predacious hyphomycetes that prey on animals other than nematodes. Here again there are no specialised organs of capture; the rhizopods appear to stick to the hyphae of the fungus which thrusts a branch into the mouth of its victim, the branch then giving rise to a haustorial system within the animal (41). Other hyphomycetes preying on rhizopods are known. *Pedilospora dactylopaga* has short adhesive processes at intervals on its hyphae, by means of which it is able to capture individuals of *Difflugia globulosa* and *Trinema enchelys* (31). More nearly allied to the main series of predacious hyphomycetes is *Dactylella passalopaga* which craftily makes use of the feeding habits of the rhizopods on which it preys in order to bring about their undoing. The animal concerned is *Geococcus vulgaris,* a testaceous rhizopod which commonly feeds on *Pythium* oospores by applying its mouth to the oospore wall and sealing the contact with a yellow secretion which is apparently similar to the substance used to close up the test during encystment. When the protozoan is rash enough to apply this technique to filaments of *D. passalopaga,* the fungus responds by thrusting a lateral branch into the mouth of the animal, and the branch then expands to form a simple or lobed enlargement which is wider than the orifice. The animal is thus unable to withdraw, and its death and absorption by the fungus ensue (38). *Eughypha levis,* another testaceous rhizopod, is also captured by *D. passalopaga.* This piece of opportunism on the part of the fungus suggests the interesting possibility that the capture of amoebae by mycelial Zoopagaceae may be something of like nature, the initial attack coming from the amoeba, not from the fungus.

Dactylella tylopaga also captures Protozoa, the victims here being amoebae (35). The hyphae of the fungus bear rounded adhesive processes; when an amoeba has stuck to one of them, an extensive haustorial system of twisted hyphae is formed within the endoplasm, which is progressively absorbed. The unusual conidia of this species, with their empty appendages and short branched conidiophores, make its inclusion in the genus *Dactylella* open to doubt.

It is rather strange that in the *Arthrobotrys* series of predacious hyphomycetes only one species has been recorded as capturing arthropods. *Arthrobotrys entomopaga* is predacious on spring-

tails (*Collembola*) which it captures by means of short adhesive processes (54). This interesting species has so far been found only in America.

ENDOZOIC PREDACIOUS HYPHOMYCETES. The endozoic predacious hyphomycetes are a rather mixed group, having the common character that the main vegetative mycelium is within the body of the host, only the fertile hyphae being external. They attack nematodes, infection usually being brought about by means of adhesive spores which stick to the integument of the animal on casual contact. As the spores are commonly produced in large numbers, and as the host animals are numerous and gregarious, substantial epizoötics may ensue, at any rate in Petri dish cultures. Two of the commonest of the predacious fungi, *Harposporium anguillulae* (107) and *Acrostalagmus obovatus* (48), are included in this group. The conidia of the endozoic hyphomycetes are usually small, slimy phialospores being common. The genus *Nematoctonus*, with clamp connections on its fertile hyphae, is unique in this series; it is probably an imperfect basidiomyete.

Harposporium anguillulae is very common in soil and in decaying plant material of various kinds. Nematodes are infected by means of spores which stick to their integument. The spores are sickle-shaped, the proximal end being pointed and the distal end bluntly rounded; adhesion to the eelworm probably depends on the presence of a sticky substance, though it has been suggested (99) that the skin of the animal may be penetrated by the pointed end of the spore. Multiple infection is not unusual. On germination the spore produces a germ tube that penetrates the integument of the host and gives rise within it to a mycelium of sparingly branched septate hyphae. The mycelium continues to grow at the expense of the host which, after becoming increasingly sluggish in its movements, eventually dies. Finally the entire contents of the nematode are consumed by the parasite, leaving the integument filled with mycelium.

Sporulation occurs freely after the tissues of the animal have been used up. A lateral branch from the mycelium forms a pyriform swelling just beneath the integument of the host. From this an apical outgrowth penetrates the integument and grows out from it as a fertile hypha, consisting usually of from two to four cells, though exceptionally it may be longer. The fertile

hyphae are usually bluntly rounded at the distal end and somewhat constricted at the proximal end where they issue through the integument of the animal, and they bear laterally, singly or in groups, subspherical phialides, each with a short, slender neck, which may be somewhat curved. Each phialide produces in succession usually from one to five spores which are elongated and sickle-shaped. Many fertile hyphae are formed, and the conidia are very numerous, littering the surface of the substratum. In agar cultures, epizoötics due to *H. anguillulae* often persist for a long time, usually being terminated by the drying up of the culture.

In addition to the fertile hyphae bearing conidia, the mycelium within the host sometimes forms chlamydospores. These are somewhat swollen, thick-walled cells, formed sometimes singly, but much more commonly in rows of three to six or more, by the swelling of cells of the vegetative mycelium and deposition within them of abundant cytoplasm, followed by thickening of the cell-walls. Sometimes chlamydospores are formed outside the body of the host on short lateral branches of the mycelium similar to those on which the fertile hyphae originate. Under moist conditions these chlamydospores germinate, producing fertile hyphae bearing phialides and spores. The formation of spores in *H. anguillulae* has been fully described by Karling (96).

Six other species of *Harposporium*, all attacking nematodes, have been described from England (26, 27) and America (48, 60, 69). In *H. oxycoracum* (48) the fertile hyphae are longer than in *H. anguillulae,* and so are the spores, and each spore has at its distal end a small droplet of apparently adhesive fluid; this latter feature also appears in *H. helicoides* (26, 48), with even longer spores. In *H. diceraeum* (48) the very small conidia are sharply twisted, while in *H. bysmatosporum* they are shaped like a human upper arm bone; the latter species also differs from the others in that infection of the nematode is by the mouth (60). The delicate *H. lilliputanum* (26) has rather long fertile hyphae; the conidia resemble those of *H. anguillulae* in shape and are very small. *H. subuliforme* has awl-shaped spores, from the tips of which short adhesive spurs are put forth obliquely (69).

The endozoic species of *Acrostalagmus* attack nematodes in the same manner as *Harposporium. A. obovatus* (48) is extremely

common; I have observed it in garden compost, soil, leaf-mould, decaying plant stems, cow-dung and rotting wood, and it is by no means uncommon in decaying plant material in water (Peach, personal communication). The mycelium consists of branched, septate hyphae which fill the integument of the nematode, having absorbed its contents. From the internal mycelium, fertile hyphae are given off as lateral branches which grow out from the carcass of the eelworm to a length of up to half a millimetre; they are irregularly septate and may be prostrate or somewhat ascending. The fertile hyphae bear at intervals flask-shaped phialides, formed singly or in groups, at the apex of which the slimy phialospores are produced successively, cohering round the distal end of the neck of the phialide in groups of up to twenty. The spores are ovoid to sub-spherical, and very small. The spores adhere to the exterior of passing nematodes, their germ tubes penetrating the integument and giving rise to the internal mycelium. As the spores are produced in large numbers, chances of infection are good, and in plate cultures nematodes are frequently seen moving about actively with many spores adhering to their skins, especially near their anterior ends.

Several other species of *Acrostalagmus* are known to attack eelworms. In *A. gonioides* (48) the fertile hyphae stand erect or ascending, and the phialides on the aerial portions are usually arranged in whorls. *A. zeosporus* (58) has phialospores shaped somewhat like maize grains, while in *A. bactrosporus* (48) they are cylindrical. In both *A. tagenophorus*, which attacks rotifers, and *A. gonioides* in eelworms, chlamydospores may be present (50), formed on short hyphae outside the host.

The validity of the genus *Acrostalagmus* is open to doubt. Those species in which the phialides are arranged in whorls could be accommodated in *Verticillium*, but *Acrostalagmus obovatus*, where the phialides are not verticillate, is difficult. Since all these species are clearly related and have pronounced characters in common, the best solution would probably be to place them in a genus on their own.

Verticillium sphaerosporum, recently described as attacking the stem eelworm (*Ditylenchus dipsaci*) in diseased *Calceolaria* plants from Scotland (86), closely resembles *Acrostalagmus obovatus*, but its spores are more nearly spherical and the phialides are

mainly in whorls on ascending fertile hyphae. Another not un-
common fungus, closely related to the various species of *Acrosta-
lagmus,* is *Spicaria coccospora* (48) ; it differs from *Acrostalagmus*
in that the conidia, instead of forming a group round the tip of the
phialide, are in chains. Like *Acrostalagmus,* the validity of the
genus *Spicaria* is dubious.

Cephalosporium balanoides (48) resembles *Acrostalagmus
obovatus* in its general organisation, and also attacks nematodes.
It differs in its phialides, which are cylindrical rather than flask-
shaped, on long prostrate fertile hyphae. The spores are markedly
triangular in outline.

The species of *Acrostalagmus, Verticillium* and *Spicaria* de-
scribed above, and, perhaps, of *Cephalosporium balanoides* appear
to form a closely related group; they should probably be regarded
as congeneric. Like them in vegetative organisation but totally
different in its manner of spore production, is the interesting fungus
Meria coniospora which has been recorded attacking nematodes
both in England (73) and America (48). Infection of the host
is brought about by adhesive spores, and the usual endozoic my-
celium of septate hyphae develops. After death of the animal,
rather short fertile hyphae emerge; these are procumbent or
ascending and bear small conical spores on fine sterigmata. The
spores are flattened at their broad basal end and pointed at the
apex which often bears a tiny globule, possibly of some sticky
substance to enable the spore to adhere to the skin of a nematode.
Nematodes can often be seen in cultures, moving about with large
numbers of the conidia sticking to them, and the conidia are not
removed by the worms brushing against solid objects that lie in
their path. The production of spores on sterigmata instead of on
phialides seems to place *Meria coniospora* rather apart from the
endozoic hyphomycetes so far described.

Far removed from the other predacious hyphomycetes is the
genus *Nematoctonus* with its relatively large conidia formed on
lateral sterigmata and clamp connections on its fertile hyphae.
N. tylosporus (48) forms a mycelium of branched septate hyphae
in nematodes, following infection by an adhesive spore. After
death of the host, fertile hyphae grow out from its carcass to a
distance of a millimetre or more. They bear fusiform conidia on
short lateral sterigmata ; these conidia, which are of the order of

20 microns long and two or three microns wide, are more massive than those of any of the endozoic species described above. The conidia are attached to the sterigmata by their broader proximal ends, while at their distal ends they carry a small knob which is probably adhesive. Sometimes the knob is replaced by a short process, probably formed by premature germination, which according to Drechsler (48) is highly adhesive. By means of either the knobs or, more usually, the apical processes, the conidia stick to nematodes and, on germination, the skin of the animal is penetrated; from the penetration tube the internal mycelium is derived. In addition to the conidia, the fertile hyphae may bear ovoid, yellowish, spore-like bodies. These are probably resting spores.

The most interesting feature of *N. tylosporus* is the presence of well-formed clamp connections on the fertile hyphae. These differ in no way from the typical clamp connections of the Basidiomycetes, and suggest strongly that *Nematoctonus* may be an imperfect representative of that group. Nothing is recorded concerning the nuclear condition in *Nematoctonus;* in view of the presence of clamp connections, it would be interesting to know whether the cells are dicaryon. Several other species of *Nematoctonus* have been described (48, 52, 56, 66), all attacking nematodes.

OTHER PREDACIOUS FUNGI. Nearly all the predacious fungi that are at present known are referable to one or other of the two major taxonomic groups which have already been described. There are, however, a few interesting phycomycetous species which, in their organisation for the predacious life, have many features in common with the Zoopagaceae and the predacious hyphomycetes, though they are unrelated to either.

Zoophagus insidians was one of the earliest predacious fungi to be described (1, 125). It has since been recorded from Austria (85, 125), Jugoslavia (85), France (111), Bulgaria (1, 128), America (95, 126) and England (4). The mycelium consists of fairly delicate, non-septate hyphae, occurring in water, often among and upon algae. The hyphae bear at intervals short, unbranched, peg-like processes, by means of which rotifers are captured. The tip of the process bears a mucilaginous secretion to which rotifers appear to stick, a hyphal outgrowth from the fungus then giving

rise to a tangle of absorptive hyphae within the animal. In this mechanism *Zoophagus* shows analogy both with the Zoopagaceae and with hyphomycetes such as *Dactylella lobata* and *D. cionopaga*.

Accounts of reproduction in *Z. insidians* are conflicting in the extreme. Arnaudow (1) describes the formation of biflagellate zoospores matured in a vesicle extruded from a filamentous sporangium, while Giklhorn (85), who also observed biflagellate zoospores, claims that the sporangium was globular and that no vesicle was formed. Still more confusing is the later description (3) of bodies which were probably conidia. This observation is particularly interesting, since it may well be that two or more different fungi have been concerned and that one was a member of the Zoopagaceae. Some uncertainty is also attached to the sexual reproduction in *Z. insidians;* fertilisation of a spherical oogonium by an antheridium has been described, but here again the possibility of confusion can not be ruled out of account.

Zoophagus tentaculum has been described from America (95). Here the organs of capture consist of stout lateral outgrowths, each having at its apex a number of slender tentacles. This species reproduces by means of fusiform conidia, formed acropetally on long hyphae, suggesting strongly that its affinities lie very close to the Zoopagaceae. Sparrow (127) places *Zoophagus* tentatively in the Pythiaceae.

Another rotifer-capturing phycomycete, *Sommerstorffia spinosa*, was first observed near Sofia (2). Rotifers were infected by spores which entered by the oral passage; these germinated and produced an endozoic mycelium from which hyphae grew out of the dead host into the surrounding water. These hyphae bore lateral branches, the tips of which were engulfed by other rotifers, which became captive. Spores were produced by the mycelium within the captured animal and discharged to the exterior. The spores encysted at the mouth of the discharge tube, later producing biflagellate swarmers. Sexual reproduction, by fertilization of an oogonium containing a single oosphere, was also recorded.

A quite different kind of organisation is found in *Protascus subuliformis* (11, 73, 97, 109, 110) which is endoparasitic in nematodes. Infection is achieved by one of the club-shaped non-motile spores of the fungus becoming attached by its pointed end to the integument of a nematode. The contents of the spore pass into the animal, forming within it a subspherical or ovoid mass of

protoplasm which gradually grows and elongates to form a wide, irregularly filamentous thallus, which later becomes divided by a few septa. The thallus grows at the expense of the animal which at first seems little the worse for the presence of the parasite. Eventually, however, the nematode becomes increasingly sluggish and stiff in its movements and finally dies, usually in an extended position. In the later stages of its development the thallus of the fungus breaks up into its individual cells, each of which may become a sporangium or a gametangium.

During the vegetative phase the segments of the thallus are filled with cytoplasm, but as the time for development of spores approaches, a large central vacuole appears, the peripheral cytoplasm then segmenting to form spores. These are club-shaped, slightly curved, with the wider end bluntly rounded and the narrower end pointed, and they are usually arranged in the sporangium with their rounded ends towards the exit canal. This develops while cleavage in the sporangium is beginning; a process from the sporangium grows out through the integument of the dead animal to the exterior and, when the spores are ready for discharge, its tip opens, apparently by deliquescence. The spores are ejected forcibly, and usually when the nematode has died on the surface of an agar culture the ejected spores lie in a compact group, well clear of the mouth of the exit tube. The mechanism of this ejection is not clear; it has been suggested (110) that the spores are forced out by cytoplasmic contractions in the sporangium, but in the specimens that I have observed it did not appear to me that there was sufficient residual cytoplasm after delimitation of the spores to accomplish this. Possibly some turgor mechanism is involved, a suitable osmotic force being provided perhaps by hydrolysis of some substance such as glycogen.

Spores are produced in large numbers and, lying on the surface of the substratum, they are readily picked up by nematodes. They adhere firmly to the integument of the eelworm by their pointed ends, probably by virtue of a sticky secretion, though no adhesive fluid is visible under the microscope. In agar cultures infected by *Protascus* it is a common sight to see nematodes moving freely with 20 to 30 spores attached to them, mostly at the anterior end. In older cultures, where there are plenty of spores about, multiple infection is common.

Sexual reproduction takes place by conjugation between two

thallus segments; whether the conjugating segments belong to the same or to different thalli is difficult to observe. Protuberances put out by the two conjugating segments meet and fuse, the contents of one gametangium passing into the other. The sexual process is usually slightly anisogamous. The oospore, rounded and with a thick wall, develops within the " female " gametangium which is usually slightly the larger of the pair. The zygote then passes into a resting stage and is finally set free by decomposition of the remains of the nematode. In old cultures lines of resting spores often mark the spot where a nematode has been killed, all traces of the animal itself having vanished.

Protascus subuliformis is probably best placed in the Lagenidiales (97) but is separated from most other members of the group by its non-motile spores. Transition from a zoospore to an aplanospore is a logical step for a fungus parasitic in a host which is both highly gregarious and actively motile; in such circumstances spore motility might even be a biological disadvantage compared with the greater efficiency of an adhesive spore, and it seems worthwhile to note here the curious fact that, although eelworms are common in moist habitats, very few of the numerous fungi known to attack them have motile pores.

Myzocytium vermicolum, also parasitic in nematodes, has many features in common with *Protascus* and was first described 70 years ago (130). As in *Protascus,* the thallus within the nematode consists of a stout, irregular filament, which becomes divided at maturity into a number of cells, the filament being somewhat constricted at the septa so that the individual cells are barrel-shaped in outline. The cells do not separate. Each cell becomes a zoosporangium, the cytoplasm surrounding the central vacuole cleaving to form biflagellate zoospores, while a lateral process from the zoosporangium develops into an exit canal, growing through the integument of the dead host and liberating the zoospores outside. The zoospores, in the specimens that I had under observation, completed their development in the zoosporangium, no vesicle being formed; this conflicts with the account given by the author of the species (130) but agrees with a later report from France (12). After liberation the zoospores swarm for a few minutes, after which they usually encyst. Not uncommonly, instead of swarm spores emerging from the zoosporangium, non-motile bodies are formed, having the appearance of zoospores that have ger-

minated to produce a yeast-like bud at one end. Often two or three of these bud-like structures are formed in a chain. Whether these are in fact zoospores that have germinated (97) or whether they should be regarded as aplanospores remains to be determined; the latter view accords with the fact that in the two probably closely related species, *Protascus subuliformis* and *Haptoglossa heterospora,* the spores are always non-motile. The development of an aplanospore from a zoospore might well be an adaptation to parasitism of such a gregarious and highly motile host as a nematode. Whatever the nature of these bud-like excrescences, they appear to act as adhesive organs for attachment of the spore to the host, for I have observed spores clinging to nematodes by means of them.

Haptoglossa heterospora was first described from America by Drechsler (46), and has recently been observed in Denmark by Shepherd (personal communication). I have found it in soil in England. It forms an ovoid or rectangular thallus in nematodes, a single eelworm often containing numerous thalli. It is holocarpic, the whole thallus becoming a sporangium at maturity. The spores are globular or angular; they are non-motile, and each spore is provided with a lobed " infective body " by means of which it adheres to the integument of a nematode, thus recalling the bud-like structures in *Myzocytium vermicolum.* A remarkable feature of this fungus is that it has spores of two sizes; a given sporangium may contain large or small spores, but apparently not both. The reason for this peculiar habit is not known.

A remarkable member of this series of endozoic Phycomycetes is *Gonimochaete horridula* (59). The thalli are parasitic in nematodes, often large numbers of them in a single worm. The exit tubes are long and hypha-like, often ascending from the carcass of the host and presenting a bristly appearance. The spores are cylindrical and small, and are usually expelled, not very forcibly, from the exit tubes, two, three or four at a time; they may be held aloft for a while at the end of the exit tube. After discharge each spore develops a bulbous outgrowth which is adhesive, enabling the spore to stick to the exterior of the host.

Protascus subuliformis, Myzocytium vermicolum and *Haptoglossa heterospora* are probably best placed together in the Lagenidiales, though it is not here suggested that they are closely

related. They differ from other members of the alliance in their non-motile spores, but it has been suggested that this modification may well be an adaptation to their requirements for successfully attacking nematodes. The long exit tubes of *Gonimochaete* are remarkable, and it is difficult to see what biological advantage, if any, they secure for their possessor. *Gonimochaete* is placed by its author tentatively in the Entomophthorales, but in its holocarpic organisation and endogenous spore production it shows strong affinities with the Lagenidiales.

Three Lagenidiales which attack rotifers have been described from Brazil (98). These are *Lagenidium microsporum, L. parthenosporum* and *L. distylae,* all occurring in the Amazon valley. All three of them parasitise species of *Dystyla,* and *L. parthenosporum* also occurs in nematodes.

Lastly in this phycomycetous endozoic series we have *Meristacrum asterospermum.* The mycelium within living nematodes consists of a broad filament which may be as much as half a millimetre long, but which normally breaks up into segments with rounded ends. Each segment may form conidia or an azygospore. The conidiophores produced from the segments emerge from the host and rise erect into the air, bearing laterally sessile obovoid conidia which are formed in basipetal succession. These conidia, when abstricted, adhere to nematodes and thus spread the infection. Sometimes, instead of a fertile hypha bearing conidia growing out from a segment, the protoplasm of the segment collects into the centre of the cell and, rounding off, is surrounded by a somewhat undulating wall enclosing a subspherical protoplast. This is evidently a resting spore and is probably to be regarded as an azygospore.

The segments into which the mycelium of *Meristacrum* divides appear to be comparable with the hyphal bodies characteristic of many of the Entomophthorales, such as *Empusa muscae.* Affinity of this species with the Entomophthorales is further supported by the asexual reproduction by means of conidia, and by the presence of azygospores.

PHYSIOLOGY

The physiology of the predacious fungi has been very little studied, most of the work that has been done having been concentrated on the trapping mechanisms of the predacious hyphomycetes. Such problems as the special nutritional requirements

that may have resulted in or resulted from the predacious habit have not been touched.   An interesting field for research is vacant here.

The networks, adhesive knobs, constricting rings and other adaptations by which the predacious hyphomycetes capture their prey have long been a source of interest, though the volume of work that has been done on their physiology is relatively small. It is well known that most of these fungi do not form traps when grown in pure culture, trap formation being initiated when nematodes are added.   Some species, however, appear to be able to produce traps independently of the presence of eelworms, although more traps may be formed if worms are present.   *Dactylella cionopaga* produces its adhesive branches in pure culture on maizemeal agar, but the rather similar *D. lobata* does not (79).   *D. ellipsospora* is another species that does not always depend on the presence of nematodes for the formation of its adhesive knobs. Reticulate species normally do not form networks in pure culture, but I have recently found that a number of isolates of *Arthrobotrys robusta* and *Trichothecium cystosporium* in my own culture collection are showing a strong tendency to do so, though the reason for this unusual behaviour is not apparent.   Species with constricting rings do not normally form their traps without appropriate stimulation, though an occasional ring may be seen in pure culture.

The presence of actual nematodes is not necessary for trap formation, for it has been found that a sterile filtrate of water in which nematodes have lived will usually act as a stimulus.   This was very clearly demonstrated by Comandon and de Fonbrune (8).   These workers experimented on four nematode-trapping hyphomycetes, *Arthrobotrys oligospora, Dactylella bembicodes, D. ellipsospora* and *Dactylaria brochopaga,* which they grew in pure culture on beer-wort agar.   Spores were formed abundantly but not organs of capture, except sometimes by *D. ellipsospora.* Traps were numerous in eelworm-infected cultures.

The part played by nematodes in the initiation of the traps was verified by adding living sterile nematodes to the cultures, the sterile worms being obtained by isolating eggs from soil and sterilizing them by treatment with 10% hypochlorite solution. After some hours the eggs hatched, and the young worms could live for several days on agar without contamination with bacteria.

It was found that addition to cultures of the fungi of a little water in which sterile nematodes had lived was sufficient to stimulate trap formation, but that both nematodes and water lost this activating power after boiling. It would seem, therefore, that the stimulus to trap formation was due to some diffusible substance produced by the eelworms, and that this substance was heat-labile.

Later experiments in America (10), using *Dactylella bembicodes* as the test fungus, have suggested that the pH of the medium may play a part in constricting ring formation. The fungus was isolated from semi-decayed pine wood, where it formed abundant mycelium and many rings, into pure culture on maltose peptone agar. No rings were formed in pure culture. Addition of a drop of the brownish water from the original dish containing nematodes and fungus caused ring formation to occur within 24 hours. It was observed that this water was acid, so the effect of acidifying pure cultures of the fungus was tried. Addition of 0.1 ml., 0.2 ml. and 0.5 ml. of deci-normal phosphoric acid, respectively, to 20 ml. of maltose-peptone agar had no effect; but when 1 ml. of acid was added, many rings appeared. Other experiments on the same lines showed that growth was more abundant and trap production greater on Bladeslee's No. 230 agar than on acidulated maltose-peptone agar, while on potato dextrose agar growth was still more luxuriant but ring formation was suppressed. It was also observed that trap formation increased as available food in the medium was reduced.

Further experiments in France have extended the list of substances capable of stimulating trap formation (120). Working on *Dactylella bembicodes,* the French experimenters attempted a quantitative evaluation of the effect of various substances in stimulating ring formation, the potency of a given substance being estimated by the number of rings produced on a ten-centimetre Petri dish. Having observed that infection of the cultures by certain bacteria could act as a stimulus, they used sterile solutions in some of their experiments. They found that sterile human blood serum was a powerful stimulus to trap production, while sterile rabbit serum and sterile human urine were less effective. In a later series of experiments (22) a number of vegetable extracts was tried, always with negative results, while various substances of animal origin, namely, serum, extracts of different organs and even certain living unicellular organisms such as

Euglena gracilis, reacted positively. Guinea pig serum gave a positive reaction in a dilution as high as one part in a thousand when tested against *D. bembicodes,* and the active principle was found to be thermostable, resisting a temperature of 120° C. for one hour and a half; it was not entirely destroyed by treatment with alcohol.

Drechsler (30) has observed that constricting ring formation in pure cultures of a predacious hyphomycete, probably *D. bembicodes,* was initiated as a result of infection of the culture by mites, and he suggested that the effective factor was friction on the mycelium, produced by the mites walking across it; in view of the French work, however, it is possible that the presence of animal protein or some other substance brought in by the mites was the causative agent. The same phenomenon has been observed in mite-infested cultures of *Dactylella acrochoeta* (71).

The operation of the traps in the predacious hyphomycetes was the subject of brilliant research by Comandon and de Fonbrune (8), using a very sensitive pneumatic micromanipulator of their own design. Four hyphomycetes were used in these experiments —*Dactylaria brochopaga, Dactylella bembicodes, D. ellipsospora* and *Arthrobotrys oligospora.* They also used *Stylopage hadra,* a nematode-capturing member of the Zoopagaceae which does not form specialised traps. Microcultures of the fungi were prepared on a thin cellophane membrane soaked in nutritive fluid and spread out beneath the cover glass in an oil chamber; when the mycelium was sufficiently developed, nematodes were introduced, and traps were formed in sufficient quantity in about 24 hours.

Experiments on the constricting rings were conducted mainly with *Dactylaria brochopaga* as test fungus, but the mode of action appeared to be the same in *Dactylella bembicodes.* To observe the capture of an eelworm under the microscope, one of the worms was picked up in a micro-pipette made so that its cavity had a diameter less than that of the middle of the worm, which was retained by suction with its posterior end in the pipette. The nematode was then introduced into the ring by means of the micromanipulator. On rubbing the inside of the ring with the eelworm, the ring closed quickly by the swelling of the three cells of which it was composed, and gripped the nematode so firmly that the mycelium could be torn without disengaging the worm.

It was found possible by mechanical stimulation to make the

traps work without the presence of nematodes, and this enabled movements inside the cells of the ring to be studied under the highest powers of the microscope. A ring was placed by the micromanipulator horizontally in contact with the lower side of the cover glass of the oil chamber in order to facilitate microscopical observation. If the outside of the ring was rubbed with a micro-needle, nothing happened, but if the needle was inserted inside the ring and one of the three cells was gently rubbed, the stimulated cell quickly swelled towards the inside. Cinematographic measurements showed that its volume was more than trebled in less than one tenth of a second. Usually, a fraction of a second later, the other cells of the ring reacted without having been touched, indicating that the tactile stimulus could be transferred from cell to cell. On closure of the ring the needle was gripped so tightly that it could not be withdrawn.

Study of cinematograph films taken during the experiments showed that the increase in volume was accompanied by rapid swelling of a number of vacuoles in the cells of the ring, which took place some seconds after the explosive dilatation of the trap. A captured eelworm removed complete with ring and placed on sterile agar was absorbed, and a new mycelium was formed from hyphae derived from the ring.

The sticky mechanisms of *Dactylella ellipsospora, Arthrobotrys oligospora* and *Stylopage hadra* were studied by similar methods. It was observed that *D. ellipsospora* sometimes formed its adhesive knobs in pure culture, but that they were more numerous in the presence of eelworms. Nematodes placed by the micromanipulator in contact with the knobs adhered rapidly and firmly, and in a few seconds could not be detached. Not all the knobs were equally sticky, and it appeared that adhesiveness reached a maximum at a certain period in the life of the hyphae that bore them. Certain species of nematode did not stick to knobs that were highly adhesive for others. Only nematodes, among all the objects tested, stuck to the knobs; these objects included a glass micro-needle, the chitinous exoskeleton of insects, the surface of tiny oligochaete worms and various other things.

With *Arthrobotrys oligospora* it was found that the sticky networks were formed only in the presence of nematodes. The whole surface of the network was adhesive. The observations made with

D. ellipsospora were true in general of *A. oligospora;* all species of eelworm were not caught, there was an optimum age for adhesiveness, and objects other than nematodes did not stick. When, however, the networks were removed from a moist medium—i.e., left exposed to the air—it was found that they were adhesive to a glass needle and that a sticky substance which hardened rapidly was visible.

When a point on the cell-wall of one of the cells of a network was gently rubbed with the point of a micro-needle, the protoplasmic granules near that point were observed to move faster, and this excitation was communicated to the entire protoplasm of the cell and sometimes to that of adjacent cells. At the same time these granules moved towards the point stimulated and collected round the edges of large hyaline vacuoles that were present in the cells. A similar phenomenon was observed in *Stylopage hadra.*

S. hadra possesses no specialised organs of capture, but the whole surface of the mycelium was found to be adhesive for certain species of nematodes. Adhesiveness reached a maximum at a certain stage in the growth of a mycelial filament. Eelworms coming into contact with a hypha of the fungus appeared to be held by the secretion, around the point of contact, of a substance which solidified rapidly; the existence of such a substance has been noted by Drechsler (34). Local stimulation of the surface of a hypha produced a protoplasmic reaction similar to that observed in *Arthrobotrys oligospora;* but here, the hyphae being non-septate, the excitation was transmitted to some distance on each side of the point stimulated, with a measurable velocity. The reaction could be produced by rubbing with, or pressure by, a micro-needle, and it seems as though the accumulation of granular protoplasm that results is related to the secretion of the sticky substance that holds the nematode.

A year before the work described above, some less extensive experiments were carried out in America (10) on the mode of operation of the constricting rings in *Dactylella bembicodes.* Nematodes were added to a Petri dish culture of the fungus, and their capture by the constricting rings was observed microscopically. In fresh cultures, closure of the rings was very rapid, but in old cultures they appeared to lose their sensitivity. Since

the vigorous movement of nematodes suggested that the stimulus producing closure of the rings was a mechanical one, this was tested by inserting a fine glass hair into a ring under the microscope, the hair then being moved backwards and forwards to imitate the movement of a nematode. In no case could more than a slight swelling of the ring cells be obtained. This observation is in direct contradiction to the findings of the French workers, and it is hard to understand why this should be so. One can only say that nobody who has seen the remarkable film produced by Comandon and de Fonbrune could reasonably doubt the accuracy of their statement that closure of the rings follows stroking with micromanipulator needle. Probably some slight difference in the physiological state of the cultures used by the experimentors would account for the discrepancy.

Observations were also made on the effect of certain chemical substances on the rings. Weak solutions of potassium hydroxide and also of phosphoric, acetic, hydrochloric, sulphuric and lactic acids were applied to the rings. It was found that treatment with 1% lactic acid produced a slight swelling of the ring cells, but in no instance could complete closure be obtained. It was, however, found that complete closure of the rings could be produced by heat, applied by dropping water at a temperature between 33° C. and 75° C. on to them; below 30° C. no swelling occurred, while about 80° C. the cells were killed. Dry heat from a hot needle held near the rings was also effective. Cells swollen by hot water or dry heat were seen to contain a refractive substance, thought to be gelatinous or colloidal in nature, and it was suggested that swelling of the cell may be due either to rearrangement of molecules of water and colloidal material already in the cell, or to imbibition of additional water from the stalk; the speed at which closure took place was considered to favour the first view.

While the experiments described above shed a great deal of light on the nature of the stimuli that can induce closure of the rings, the mechanism by which the swelling is actually achieved is still a complete mystery. The speed of the reaction is against the idea of a turgor mechanism dependent on intake of water either from the hypha subtending the ring or from the surrounding medium, and the theory that the phenomenon results from molecular rearrangement of cell colloids, probably involving water

already contained in the cell, seems to be the more likely. Such mechanisms are known, or suspected, to exist in the higher plants, and could at least theoretically occur in the fungi. The constricting ring mechanism offers an attractive line of research for a plant physiologist, with the possibility that the knowledge of cytophysiological phenomena gained in elucidating the problem might have a far wider sphere of application than that of the predacious fungi alone. In this connection it might not be unduly fanciful to suggest that the mechanism of the constricting ring could be of more than passing interest to the student of stomatal movement in higher plants.

Apart from *Stylopage hadra,* the means by which the mycelial Zoopagaceae capture Protozoa have not been experimentally studied. Secretion by the hyphae of a yellowish adhesive material has been reported on a number of occasions by Drechsler, and it enters into his diagnoses of some of the genera (33). This adhesive substance is not always visible. Amoebae can cling with great tenacity to solids; it has been stated (87) that they may even remove minute fragments from a glass surface on which they are moving. Amoebae in plate cultures have an irritating habit of ranging themselves alongside fungal hyphae, simulating capture by predacious fungi where none exists, and thereby wasting the time of the observer; it is not impossible, therefore, that in some instances it may be the amoeba that is clinging to the fungus instead of the converse. This certainly seems to be the way in which capture of *Geococcus vulgaris* by *Dactylella passalopaga* (38) is effected. I have observed that old mycelia of *Stylopage rhicnacra* (77) and other Zoopagaceae often have the remains of captured amoebae, whose contents have been almost completely absorbed, attached only by the haustoria, all contact of the ectoplasm of the amoeba and the main hypha of the fungus having been broken. While one could not justifiably infer from this the absence of sticky material, it is suggestive.

The temperature relations of predacious fungi have not been studied, though some incidental observations by Drechsler are interesting. He points out that cool humid weather is favourable for the development of predacious fungi in laboratory cultures (64), a statement with which I wholly concur, although individual species vary in their preferences. *Dactylella gephyropaga* is re-

ported to grow actively and to capture nematodes abundantly at temperatures of 25–30° C., while *D. cionopaga* is almost totally inactive (67); at 15–18° C. the effect is reversed. This may be correlated with the northern distribution of *D. cionopaga* compared with *D. gephyropaga* (67). In the same way *Dactylaria psychrophila* appears to be more heat-tolerant than *D. thaumasia*. The development of thalli of *Cochlonema agamum* in amoebae is said (57) to occur rapidly at 23° C., while reduction of the temperature to 15° C. seems to inhibit the fungus and to favour recovery of the amoeba.

The constricting rings of the predacious hyphomycetes appear to have a strong tendency to take up a position perpendicular to the substratum. The biological advantage of this is clear, since it places the ring in the best position for ensnarement of nematodes, but the mechanism that ensures correct orientation has not been investigated. Geotropism can hardly be involved as the surface may not be horizontal, and the existence of a phototropic response, besides being unlikely, would seem to be ruled out, since the orientation of the rings does not depend on illumination of the cultures. Thigmotropism suggests a possible answer, and, since the rings are often placed just below the surface, a response to an oxygen or carbon dioxide gradient is not impossible. An investigation of this phenomenon might produce interesting results.

Apart from the erect position of the fertile hyphae in most species, tropic responses in the predacious fungi do not seem to be important, but it has been suggested (57) that development of the conidial chains of *Cochlonema agamum* may be positively phototropic.

The nutrition of the predacious fungi is a subject about which more information is badly needed. The endozoic species, both in the Zoopagaceae and in the hyphomycetous series, appear to be obligate parasites and have never been isolated in pure culture. Among those that capture living prey, the mycelial Zoopagaceae behave as strict predators, as Drechsler (62) points out. I have myself attempted to isolate *Stylopage rhynchospora*, *S. hadra* and a hitherto undescribed species of *Stylopage* that captures nematodes, taking advantage of the long erect conidiophores of these species to pick off spores under the microscope on a sterile needle and to transfer them to plates of maize-meal and of rabbit-dung agar. In

no instance was I successful, although in the original cultures fallen conidia were germinating freely. It is possible that germination of the spores depends on the presence of a chemical substance emanating for the host, analogous with the stimulus needed for trap formation by the predacious hyphomycetes. Such a mechanism might be of advantage to the fungus by ensuring that conidia germinate only in the presence of suitable prey, an important point for an obligate predator.

In contrast to the Zoopagaceae, the nematode-capturing hyphomycetes grow well in pure culture on most ordinary media. Both mycelial bulk and density of sporulation are usually greater than when they are growing in competition with the bacteria and other fungi that are incidental to the presence of their hosts. An animal diet is not necessary for their existence, and many predacious hyphomycetes, when growing strongly in pure culture on a rich medium, may become relatively indifferent to nematodes when the animals are offered to them. On the principle that a hungry cat is the best mouser, they should be maintained in culture on a weak medium; maize-meal agar, without added sugar, appears to suit most of them very well. In pure culture the conidia are often smaller than those formed in the presence of nematodes; thus the spores of *Arthrobotrys oligospora* have a size range of $22-32 \times 12-20 \ \mu$ when formed in nematode-infested cultures, while in pure culture on maize-meal agar this is reduced to $18-30 \times 10-15 \ \mu$ (40). The habit of sporulation may also be different in pure culture. The fertile hyphae of *Arthrobotrys oligospora* in pure culture bear their conidia in discrete whorls separated by " internodes ", the number of whorls often being a dozen or more; but when the fungus is feeding on nematodes, the conidia tend to form a single terminal head, the additional whorls appearing only in older cultures, and then being few in number. The same phenomenon occurs in *A. superba* and *A. conoides*. The reason for this is uncertain. The high nitrogen to carbon ratio resulting from an animal diet does not seem to be the operative factor, for I have found that multiple whorls of conidia are still formed in pure cultures containing meat extract or peptone, while on some high carbohydrate media, such as potato dextrose agar, sporulation may be much reduced with concomitant excessive mycelial growth.

The pH requirements of the predacious fungi do not appear to

have been studied. Adjustment of the reaction of the medium does not appear to be necessary in culturing them, and this applies both to the Zoopagaceae and to the hyphomycetes. I have observed some indication that in Nature they are less frequent in acid peaty soils, even though suitable hosts may be plentiful, but I have not sufficient data to justify any generalisation about this. Some recent laboratory experiments (Dixon, unpublished) suggest that different species of predacious hyphomycetes may differ radically in their growth reaction to changing pH, but the work is of a preliminary nature only, and no positive conclusions can yet be drawn.

An interesting correlation exists between the growth rate of the predacious hyphomycetes and the type of trap produced. Species having adhesive networks are usually faster growers than those with stalked knobs, while the constricting ring formers are slowest of all. This can be seen both in pure culture and in the presence of nematodes; in eelworm-infested plates, *Arthrobotrys oligospora* will usually make its appearance some weeks before *Dactylaria gracilis*. There does not appear to be any obvious reason for this correlation, but it does not seem unreasonable to suppose that for the production of extensive systems of networks, a vigorous habit of growth would be an advantage.

ECOLOGY

The habitat relations of the predacious fungi have been very little studied. This may in part be attributed to the general opinion that the ecology of the fungi is coincident with that of the hosts. While this assumption may be true up to a point, the evidence available at present is not sufficient to justify its adoption without investigating further, and recent unpublished work on predacious fungi in soil suggests that it may be very far from the truth.

Predacious fungi are widespread in Nature. They have been found in leaf-mould, rotting wood, decaying vegetable remains of many kinds, soil, dung, decaying plant material in water, and on and among bryophytes (78). A fungus assigned (probably incorrectly) to *Oidium* has even been reported from *Monoposthia duodecimalata,* a free-living marine nematode (7), and an internal parasite of copepods, recently observed by Sleigh, may possibly

be the first marine record of the Zoopagaceae. They may occur in the most unlikely places; a collection of soil from what was once the cellar of a bombed building in the middle of London yielded *Arthrobotrys robusta* and *Trichothecium cystosporium* (80), and in a small clump of moss (*Bryum argenteum* L.) from between paving stones outside a house several species were found (76). A recent survey (78) has shown little correlation between different kinds of habitat and the species of predacious fungi that occur, but it must be emphasised that much work will need to be done before any such correlations, if they exist, can be postulated with safety.

Leaf-mould as a substratum for predacious fungi has been widely explored by Drechsler, who has described a large number of species from this source. As a habitat for predacious fungi, leaf-mould has certain obvious advantages. An abundant fauna of nematodes and Protozoa is present, the moisture content is reasonably high and complete drying out will occur only under extreme conditions; the pH in leaf-mould from deciduous woods, moreover, is usually not too low. A certain amount of shelter is provided during hot weather, the temperature on the floor of a wood being lower than that on the ground outside. It is not surprising, therefore, that the list of species from leaf-mould is a long one. I have myself found it a good source of predacious fungi in Britain, though not so good as some others such as moss or rotting wood.

Partly decayed plant remains often contain predacious fungi, especially when lying on or near the soil. Garden compost, pieces of stem and leaf that have lain under stones, etc., old cabbage stumps and other vegetable bric-à-brac in a fairly advanced stage of decomposition, have all yielded their quota of predators. I have been fortunate enough to be able to examine some of the vegetable composts used by the late Dr. M. C. Rayner and her colleagues (117) in their work on mycorrhizal fungi in conifers, and found them very rich in predacious species, including *Trichothecium flagrans* (74). It is of some interest that this species has been detected on only two other occasions; once from garden compost at Kingston-on-Thames and once from tomato haulm compost from Manor Nurseries, near Kenilworth.

Rotting wood is one of the most prolific sources of predacious

fungi that has yet been brought to my notice. Old tree stumps, especially from fairly moist places, rotting logs lying on the ground in woods and pieces of old bark have an extensive fauna, including numerous Protozoa and nematodes, and appear also to provide a congenial habitat for many species of predacious fungi. This source had scarcely been touched until recently (26), but will amply repay further study. No attempt has yet been made to find out what ecological factors are at work, but, apart from the liberal supply of prey, the presence of moisture and, perhaps, organic compounds from the wood merit consideration. It is of historical interest that *Dactylella ellipsospora* was isolated from rotting wood as early as 1886 (88).

The predacious fungus flora of dung has hitherto received less attention than it deserves, though a number of scattered records exist. *Monacrosporium leporinum,* probably synonymous with *Dactylella ellipsospora,* was found in hare dung in Bohemia at the beginning of the present century, but its predacious activity, if any, escaped notice (6). *Arthrobotrys oligospora* has long been known to be frequent in horse dung and is often present in the milky fluid that climbs up the sides of a glass vessel in which fresh moist horse dung is allowed to stand undisturbed. There is evidence that the species present change with age, though this successional aspect has not been worked out yet, and it has been my experience that old dung, provided that it has not dried up completely, is usually richer in species than new. Among interesting predacious fungi that I have encountered in old cow dung are *Dactylella heterospora, Cystopage lateralis* and *Protascus subuliformis,* while horse dung, intended for use as garden manure, yielded on two separate occasions, *Stylopage cymosa* and *Arthrobotrys conoides.* A recent communication (94) has listed further species of predacious fungi from dung, and suggests that there are more to come.

Examination of mosses for predacious fungi was first suggested to me by Dr. B. Barnes, and has proved most fruitful. That mosses possess a rich and varied fauna of minute invertebrates, including many nematodes and Protozoa, has been made clear by a recent and very detailed study in Denmark (112). These animals are preyed upon by a rich assortment of fungi, drawn from most of the important predacious series. The source of

most of the moss-inhabiting predacious fungi is probably the soil beneath, and it seems reasonable to suppose that they grow up the moss plants from below, assisted by or in response to the presence in the moss clumps of water or animal prey or both. According to the Danish account, the nematodes tend to follow the " water table " in the moss cushions, and it is probable that the fungi do the same, though this has not been tested. As an example of the richness of the moss flora, one small collection of mosses made some years ago from the banks of a lane in Devonshire contained no less than eight species of predacious fungi (78).

Since predacious fungi are so common on and among mosses, it might reasonably be suggested that at least some of them are parasitic on the bryophytes. Although I have examined numerous specimens where both Zoopagaceae and predacious hyphomycetes have been growing and sporulating vigorously on the leaves of moss, I have never found the slightest evidence for believing that the fungi were other than harmless epiphytes.

The occurrence of predacious fungi in soil is a subject that, until recently, has been badly neglected, and this is surprising in view of the possible importance of the nematode-capturing species as a natural restraining influence on plant parasitic eelworms. In an experimental plot in Hawaii the presence of no less than 15 nematode-attacking fungi has been noted (102), and that this is nothing out of the ordinary is shown by the results of the examination of the surface layer of soil from a five-rod plot near London, where 21 species of predacious fungi were found, of which 13 attacked nematodes (Dixon, unpublished). Recent work by Shepherd in Denmark, not yet in print, has shown that a large and varied predacious fungus flora exists in the soil of that country, and my own observations during the past year on arable soil in Britain have convinced me that predacious fungi are as numerous in the soil as they are elsewhere, if not more so. It is surprising that they have not been recorded more frequently by soil mycologists, but the methods of examination used are probably unsuitable for their detection.

The soil flora includes both Zoopagaceae and predacious hyphomycetes, the *Arthrobotrys* series and the endozoic forms being well represented. The number of species in a given soil sample does not appear to be less than one would expect to find in a

collection of leaf-mould, moss or any other material in which these fungi occur. The relative frequencies of the various species in soil appears in general to be much the same as elsewhere, as far as the limited information at present available can be trusted, but there are certain exceptions to this. In a series of 49 soil samples that I have recently examined, 82 records of nematode-attacking fungi were made. *Arthrobotrys oligospora* accounted for 21 of these records, and another 18 resulted from an unidentified member of the Zoopagaceae which captured nematodes by adhesion to the mycelium after the manner of *Stylopage leiohypha* and *Cystopage lateralis,* but which formed no spores. As I have never found this latter species in any other habitat, unless it is a sterile strain of a species already known, it may be a specialised soil inhabitant. The next most frequent species in the series was *Harposporium anguillulae,* with six records, followed by *Acrostalagmus obovatus* with five and *Arthrobotrys dactyloides* with four. This striking preponderance of two species over all others is unusual.

Use of dung as an agricultural fertilizer must necessarily have a profound effect on the predacious fungus content of the soil, at least for a certain period after dunging. This has not been properly investigated, but I have observed on one occasion that a dunged plot contained a different predacious flora from an untreated control, and that this effect was maintained for at least three years after application of the dung. If nematode-attacking fungi have any effect on the plant pathogenic nematodes in the soil, this factor is worthy of serious consideration by agriculturalists.

The occurrence of predacious fungi in water has been studied intensively by Peach (113–115), to whom my thanks are due for permission to quote unpublished work in this field. An examination of water, soil and vegetable debris from various kinds of aquatic habitat has shown that both the Zoopagaceae and the predacious hyphomycetes are by no means confined to land. Some species seem to be particularly common in water or wet places; thus *Acaulopage dichotoma* was found capturing amoebae in aquatic situations on no less than 19 occasions. It may be noted that this species was originally described from waterlily leaves (33). *A. tetraceros* appeared in 16 samples from 11 aquatic habitats; the specimens of this species seemed to be of a strain with

longer and narrower conidia than the type, probably best regarded as a distinct sub-species. *A. dichotoma* and especially *A. tetraceros* are species in which the distal end of the conidium is evacuated, in *A. tetraceros* the empty portion forming from three to six filiform appendages; it seems not unlikely that added buoyancy resulting from this evacuation may be of assistance in dispersing the spores in water. Among the Zoopagaceae recorded by Peach the genus *Acaulopage* was by far the most frequent.

The predacious hyphomycetes are also well represented in aquatic habitats. Nine species of nematode-trapping hyphomycetes were identified by Peach, all the principal types of trapping mechanism being represented. *Arthrobotrys oligospora* appeared to be less common than it is in terrestrial situations, and the most frequently recorded predacious hyphomycete in the area covered by the work was *Dactylella cionopaga*. This is interesting in view of the fact that Drechsler (40) has recorded that *D. gephyropaga,* a species that captures nematodes by means of columnar adhesive branches somewhat similar to those of *D. cionopaga,* occasionally includes rotifers in its diet. There is, however, no similar record for *D. cionopaga.*

A curious feature of the survey carried out by Peach is the complete absence of such forms as *Zoophagus insidians* from her records, in spite of the fact that her cultural methods included " baiting " with boiled cress seeds. It may be that the media used in subsequent treatment did not suit their development, but it must be borne in mind that if an inventory of all the known predacious fungi is taken, the lower fungi, with the exception of the Zoopagaceae, are numerically insignificant. This is in itself surprising and difficult to explain, though two suggestions might be made: in the first place, aquatic surroundings may not be favourable for the capture of animals by trapping mechanisms, and in the second, the relatively uniform conditions of life in water may well lack the essential stimulus to evolution needed for the development of the predacious habit in more than a very small number of aquatic fungi. Whatever the reason, however, the fact remains that the predacious fungi occurring in water appear to be mainly land forms that may in some instances (*Acaulopage* spp.) have secondarily adapted themselves to some extent for aquatic life. It must also be remembered, in view of the method of spore

formation in *Zoophagus tentaculum* (95), that *Zoophagus* may not be a primarily aquatic genus.

OTHER BIOLOGICAL CONSIDERATIONS

The predacious hyphomycetes in the main show little, if any, host specificity. Most of the *Arthrobotrys* series appear to be able to capture a wide range of eelworm species, and it seems likely that the most important factor in deciding whether a particular species of eelworm is suitable prey is size. Robust predators such as *Trichothecium flagrans* are well able to cope with nematodes more than a millimetre long, while some of the more delicate species like *Dactylella asthenopaga* seldom capture worms of more than a third of that length. The nature of the cuticle of the nematode may also be of importance, for it is possible that the sticky secretions of the fungi may vary in efficiency according to whether the surface of the eelworm is smooth or striated. If this is so, its effect would probably be most important during senescence of the mycelium, when the traps are beginning to lose their stickiness. Some of the predacious hyphomycetes may even capture animals other than nematodes; thus *Dactylella gephyropaga* has been recorded (40) as occasionally capturing the rhizopod *Trinema enchelys,* the animal being caught by the mouth by an adhesive process as a result of attempting to feed off the fungus. *D. gephyropaga* has also been known to invade the oospores of *Pythium butleri* by means of lateral branches from submerged hyphae.

The endozoic predacious hyphomycetes vary in their ability to parasitise different host species. Many of them are known to attack nematodes belonging to several genera, while others have been recorded as parasitising a single species only, though here it is possible that further records may enlarge their host range. Our knowledge of most of these forms is insufficient to allow generalisations to be made.

In sharp contrast to the polyphagy of the predacious hyphomycetes, most of the Zoopagaceae are highly host-specific. It is most unusual for more than one species of rhizopod to be captured by a member of this family (62). There are, however, recorded instances of this happening. *Acaulopage ischnospora* regularly captures two species of *Amoeba,* and the same two species are

victims of *Zoopage virgispora*. It has been suggested (63) that these two amoebae may have some similarity in the composition of their protoplasm of their pellicles. It is possible, though not quite certain, that *Acaulopage baculispora* may also attack two different amoebae (64), and in this connection it is interesting to note that *A. baculispora* and *A. ischnospora* are morphologically very similar, differing mainly in the length of their spores and the amount of distal evacuation.

The members of the Zoopagaceae that capture nematodes appear to be more catholic in their taste, size being probably the most important factor in determining whether a given species of nematode is suitable for prey. It is reasonable to suppose that the limitations governing the capture of nematodes by adhesive material operate similarly for such fungi as *Stylopage hadra* and for the predacious hyphomycetes.

An example of hyperparasitism affecting a predacious fungus is found in the observation (71) that *Dactylella helminthodes,* a non-predacious species which normally subsists on *Pythium* oospores, may sometimes attack the oospores of *Cochlonema megalosomum.*

The principal genera of the predacious hyphomycetes contain species that appear to have no predacious tendencies. Thus, in addition to *Dactylella helminthodes,* mentioned above, *Trichothecium polyctonum* also attacks *Pythium* oospores, while *Dactylella strobilodes* (68) appears to be purely a saprophyte. The well-known *Trichothecium roseum* also has never been known to attack animals. A number of other instances are known; it must, however, be remembered that in the past several fungi long known as saprophytes have ultimately been shown to be predacious. Different isolates of the same species, moreover, differ in their aggressiveness towards eelworms, so that it is always possible that one worker may succeed where another has failed in showing that a given species is predacious. I have known a particular strain of a predacious hyphomycete to lose all interest in nematodes, at least for a time, when cultured under the wrong conditions; for example, *Trichothecium flagrans* when grown in pure culture on maize-meal agar may lose its power of forming adhesive networks and with it, incidentally, its ability to produce conidia. Both these faculties may sometimes be restored by

culturing the fungus on rabbit-dung agar. I can offer no explanation of this curious fact.

Spore dispersal in the predacious fungi has not been investigated. Endobiotic species usually have adhesive spores, as in *Endocochlus, Cochlonema* and the endozoic hyphomycetes, with the exception of *Myzocytium vermicolum,* which has zoospores. It is worthy of note, however, that *M. vermicolum* also produces non-motile, adhesive spores, and it has already been pointed out that for attacking a highly motile and gregarious host such as a nematode, motile spores are unnecessary and probably less effective than an adhesive mechanism. Species that attack nematodes by means of adhesive spores, therefore, can afford to rely on the motility of their hosts to secure dispersal.

The conidia of the *Arthrobotrys* series and of the mycelial Zoopagaceae appear to be quite suitable for dispersal by air currents, but in view of their habitat, earthworms and arthropods should not be ruled out as possible agents. In mite-infested cultures I have often seen the conidia of *Arthrobotrys oligospora* and other predacious hyphomycetes attached in large numbers to the hairs on the bodies of the animals, especially at the posterior end. There is no evidence that these fungi ever attack mites.

In the genus *Acaulopage* the conidia are usually provided with empty distal appendages, formed by shrinkage of the cytoplasm followed by cutting-off of the appendage by a septum. Such appendages might be of assistance in air dispersal, or they might enable the conidia to stick to animals for transport. A third possibility here, however, and one that must be given very serious consideration, is water dispersal, for the work of Peach has clearly shown that some species of *Acaulopage* have distinct aquatic tendencies. The whole subject of dispersal in the predacious fungi needs investigation.

A study of the distribution of predacious fungi shows that different species vary greatly in their range. *Arthrobotrys oligospora* and *Dactylella ellipsospora* appear to be widely distributed in both hemispheres, while some species, as far as available records show, are much more restricted. *Arthrobotrys robusta* occurs in Britain in Middlesex, Surrey, Essex, Westmorland, Warwickshire, Lincolnshire and Cambridgeshire, and is evidently a very common fungus in this country; it has not, however, been recorded by

Drechsler, which suggests that it can not be widespread in the United States. *A. musiformis* seems to be more local in its British distribution; I have found it in leaf-mould from three stations in Warwickshire, all close together, and nowhere else. It has been recorded from Denmark by Shepherd. Among the Zoopagaceae, *Acaulopage tetraceros*, *Stylopage rhynchospora* and *S. rhicnacra* are common in Britain, while no species of *Endocochlus* or of *Bdellospora* has yet been recorded as British.

The origin of the predacious habit presents a problem of great difficulty. Leaving aside such internally parasitic forms as *Protascus, Myzocytium* and the endozoic hyphomycetes, we have in the Zoopagaceae and the *Arthrobotrys* series two groups of fungi, taxonomically quite unrelated, which have both adopted a highly unusual mode of life, and which show certain resemblances to one another in their adaptations; for instance, the production of a sticky secretion for the ensnarement of nematodes in *Stylopage* and *Arthrobotrys*. Any adaptive resemblances between the two groups must be homoplastic, but it is reasonable to speculate on whether the same or similar circumstances led to both groups adopting the predacious manner of life. If wide distribution may be taken as indicating antiquity, the original adaptation must have occurred a long time ago, for *Arthrobotrys oligospora, A. musiformis, Dactylella ellipsospora* and others have been recorded from Europe, America and Australasia. The analogy between the predacious fungi and the insectivorous flowering plants is a striking one (108), and it is by no means impossible that both these groups may have adopted their peculiar mode of life in response to similar circumstances. Difficulty in obtaining adequate supplies of some essential food substance suggests itself readily as a predisposing factor, and deficiency of nitrogen seems as likely as any, though the importance of a source of carbon can not be overlooked.

ECONOMIC ASPECTS

The importance of nematodes as destructive parasites of crop plants has led a number of workers to attempt the biological control of these pests by means of the predacious fungi. For these experiments, the hyphomycetes of the *Arthrobotrys* series have been mainly used, as neither the endozoic hyphomycetes nor the Zoopagaceae lend themselves to artificial culture on the scale

needed for the work. Most of this work has been centered in Hawaii (102–106) and in France (13–25, 101, 118–123), but recently some interesting observations have come from Holland (100).

The work in Hawaii was directed against the root-knot eelworm (*Heterodera marioni*), and two methods were used. One of these was concerned with artificial stimulation into activity of natural enemies of the eelworm already present in the soil. It was found that when fresh plant material was incorporated into the soil, there was a rapid increase in the population of free-living nematodes. In one experiment, a 65-fold increase was obtained in 14 days, but, in spite of this, in 21 days the nematode population was much reduced and predacious fungi were very conspicuous. Apparently the increase in activity of the fungi overbalanced that of the eelworms. Tests showed that during such a period of increased activity the larvae of parasitic nematodes decreased in numbers. In a series of laboratory and glass-house tests, chopped pineapple plant material was mixed with naturally infected soil and allowed to decompose. In every experiment reductions in the numbers of infective *Heterodera* larvae were observed, and it was claimed that the results were statistically significant at the 0.1% level (102, 106).

Comparable results were obtained by application of other plant material, such as the grass *Panicum barbinode,* and it was suggested that this might explain the beneficial results that had been obtained by green manuring *Heterodera*-infested soils.

The second method used by the workers in Hawaii was the introduction of pure cultures of predacious hyphomycetes into soil infected with *Heterodera marioni* (105). In these experiments pineapple plants were grown in five-gallon pots of steamed soil, and three series of treatments were given. In one series nothing was added; in another the pots were infected with a known number of *Heterodera* larvae; while the third series received both larvae and an inoculation of one of six different predacious hyphomycetes. In all, the experiment comprised ten treatments, and each treatment was ten times replicated. The pots were kept under observation 15 months.

The results of the tests were disappointing. While a certain measure of control of the eelworm appeared to result from inocu-

lation with *Dactylella ellipsospora,* the other fungi used, consisting of *Arthrobotrys oligospora* (two isolates), *A. musiformis, Dactylella* sp. and *Dactylaria thaumasia,* were apparently without effect.

Much work has been done in France on the biological control of nematodes parasitic in plants (19, 25) and in domestic animals (13–16, 18, 24, 118, 119, 122, 123). In some early experiments on the eelworm causing pseudotuberculosis in horses (13) an ingenious method was devised for allowing eelworms to enter cultures of the fungi in as natural a manner as possible and with a minimum of contamination. Dung cultures containing the eelworms were covered with half Petri dishes containing agar cultures of *Arthrobotrys oligospora* and of *Dactylella bembicodes.* Pieces of filter paper were then arranged vertically in contact with the inner sides of the dishes containing the dung in such a manner that the nematodes were able to climb up them to gain entry to the fungus cultures. In this way it was possible to show that the nematodes were killed in large numbers by the fungi.

Other workers in France have demonstrated the ability of various predacious hyphomycetes to capture the larvae of eelworms parasitic in horses (118), cattle and sheep (14, 16, 18, 123), and even in the chimpanzee and in man (119). Little practical use appears to have been made of these discoveries. The fungi used were *Arthrobotrys oligospora, Dactylella ellipsospora* and *D. bembicodes.* The same three fungi were also shown to be capable of attacking successfully some of the nematodes causing disease in plants (19), and experiments on the actual control of plant pathogenic nematodes have been carried out with some success. In an attempt to control the root-knot eelworm (*Heterodera marioni*) in begonias, cultures of *Arthrobotrys oligospora* and of *Dactylella bembicodes* were added to infected compost in which the plants were growing, and it was found that the 50% infestation shown by the controls was reduced to 20% by *A. oligospora* and to 9% by *D. bembicodes* (25).

Some of the French workers have suggested methods for the preparation of fungal material in bulk, and in a form suitable for large-scale application to land. In one of these (21) the fungi were cultivated in a medium of oat straw, malt extract and agar, the spores being collected in due course, dried and distributed over the soil. In another method a liquid medium was used,

prepared from cooked maize and malt extract (24). When growth of the fungus was complete the liquid was drawn off, and the mycelium and its spores slowly dried, after which it was mixed with dry soil as a neutral medium to facilitate its distribution as a powder. I have tested the medium with *Arthrobotrys oligospora* and *A. robusta,* and have found both mycelium and spore production very good; I have not, however, tried its efficacy in the practical control of eelworms. Other methods of cultivation have also been suggested (17).

Other points arising in the pratical application of predacious fungi in nematode control have been investigated by the French school. One of these was the ability of predacious hyphomycetes to withstand lack of oxygen (23). It was thought that both *Arthrobotrys oligospora* and *Dactylella ellipsospora* were probably strict aerobes, since they grew only on the surface of liquid media, while *D. bembicodes* penetrated to a depth of 20 centimetres below the surface, suggesting a certain capacity for partial anaerobiosis. The possibility that the fungi might be potential parasites of cultivated plants was also examined, and no evidence of this could be observed when they were allowed to grow in contact with the vegetation in pastures; moreover, it was shown that animals grazing thereon took no harm from the fungi (20).

In view of some of the results obtained by the French workers, it is surprising that the possibility of using predacious fungi for the control of eelworms has not been more widely investigated, especially when one considers the immense damage to the crops of the world caused by these pests. Recently the matter has been taken up in Holland, and a description of a Pyrenomycete growing on the cysts of the potato root eelworm (*Heterodera rostochiensis*) has been described (100). During the last two years, unpublished work in my own Department has shown that the inoculation of soil with predacious hyphomycetes is a practical possibility, and that soil so inoculated retains the fungi for a reasonable period of time. Experiments have also indicated that the fungi are capable of reducing the population even of cyst-forming eelworms such as *Heterodera rostochiensis.* Much fundamental work remains to be done, however, before the value, if any, of biological control can be assessed accurately, and, as has been pointed out in an earlier communication (76), no useful

results in the practical field are likely to accrue until our knowledge of the biology and ecology of the predacious fungi has been greatly augmented.

TECHNIQUE

Many of the predacious fungi are not only very common but are also easy to grow in the laboratory. Their peculiar mode of life, however, makes them different from most fungi in some of their basic requirements, and in order to culture and observe them successfully some departures from conventional mycological technique are needed. A brief account of some of the methods that have been used in their study is presented here in the hope that it may be of help to those who wish to observe these interesting plants at first hand.

Mixed cultures of predacious fungi may readily be obtained by placing a small quantity of decaying plant material in the centre of a Petri dish containing sterile maize-meal agar. In order to prevent undue growth of moulds, the medium should be a weak one. A suitable medium may be prepared by adding 20 grams of maize-meal to rather more than a litre of tap water, and heating at 70° C. for one hour. The mixture is put aside to settle, and then a litre of clear supernatant liquid is decanted off, filtering through glass wool if necessary. To this, 20 grams of powdered agar are added, and the medium is autoclaved at 15 pounds per square inch for 20 minutes. Plates poured with this medium are suitable for nearly all predacious fungi.

After inoculation the plates are incubated at room temperature and observed periodically by examining the surface of the medium with a low power objective. Some of the more quickly growing predacious fungi may appear in about a week, while the slower ones, such as some of the hyphomycetes with constricting rings, may not be seen until two months or more after inoculation. The presence of predacious fungi can usually be recognised by the appearance of amoebae, somewhat rounded in shape, lying alongside very fine hyphae, or by dead or dying eelworms captured by predacious hyphomycetes. The characteristic conidia of both the Zoopagaceae and the *Arthrobotrys* series are often useful in detecting the presence of the fungi.

For examination of predacious fungi under higher powers of the microscope, preparations must be made. Living material is

far more satisfactory than stained specimens, and for its observation a small block of agar is cut out with a scalpel, the surface bearing the fungus being then sliced off as thinly as possible with a sharp razor blade and mounted in water, using a cavity slide so as to avoid crushing the specimen unduly when the cover glass is applied. If the specimen is to be preserved for more than an hour, the cover slip should be ringed with vaseline.

Permanent preparations of predacious fungi are not easy to make. The predacious hyphomycetes can be mounted quite satisfactorily in lactophenol coloured with a little cotton blue, but lactophenol is quite useless for most of the Zoopagaceae. Substitution of lactic acid for lactophenol allows fairly good preparations of Zoopagaceae to be made, but these do not last more than a few months.

For permanent mounts of Zoopagaceae, a method using chlorazol black is often useful, especially for showing the haustoria in amoebae. Thin slices of agar bearing the fungus are fixed in absolute alcohol for one minute, stained in a saturated solution of chlorazol black E in absolute methyl alcohol for ten minutes and mounted in Euparal, using a cavity slide. Full details of this and other methods have been given elsewhere (82, 83).

Excellent preparations of the predacious hyphomycetes of the *Arthrobotrys* series can be obtained by the Venetian turpentine method. From a block of agar the surface bearing the fungus is thinly sliced off and fixed in formalin-acetic acid (commercial formalin, 10 parts; glacial acetic acid, 5 parts; distilled water, 85 parts) for at least 24 hours. After washing until no smell of acetic acid remains, the slices are stained in Delafield's haematoxylin for a few minutes, differentiated in acid alcohol if necessary, " blued " in tap water or ammonia vapour, and placed in about five ml. of 10% glycerine in a watch glass, which is then left exposed to the air for the water to evaporate. When the glycerine has concentrated to a thick syrup, the dehydration is finished off in a desiccator. The process of concentration should take about two days. The material is then washed in absolute alcohol to remove the glycerine, and placed in a 10% solution of Venetian turpentine in absolute alcohol; this should be done in a desiccator, as the turpentine is extremely sensitive to moisture, and the material should be left in the desiccator until the turpen-

tine has thickened sufficiently for mounting. The agar slices are then mounted in an alcoholic solution of Venetian turpentine of suitable consistency, using a cavity slide.

The best preparations that I have yet obtained of the predacious hyphomycetes have been made by the following method. Blocks of agar bearing the fungus are fixed in formalin-acetic acid and washed. The block is then stuck, fungus downward, on a No. 1 cover slip by means of Szombathy's gelatine. The cover slip is left in a warm place—about 30° C.—until the agar begins to shrink, the face of the block bearing the fungus being prevented from shrinking because it is attached to the glass. At a stage in the drying process which can be determined only by experience the agar is cut away as close to the glass as possible, using a very sharp razor blade. The film of agar left on the cover slip contains the fungus; this can be stained with Heidenhain's haematoxylin, dehydrated, cleared in xylol and mounted in balsam. This method is not so difficult as it sounds, and gives superb preparations.

The endozoic hyphomycetes are difficult to handle, as the infected eelworms often succumb below the surface of the agar. Permanent preparations of these fungi are best made either in lactophenol or in glycerine jelly; for the latter technique, erythrosine is an excellent stain, and the preparations are improved if very slightly acidified with acetic acid, for this increases the brilliance of the stain.

Isolation of the *Arthrobotrys* series into pure culture presents few difficulties, since their conidia are carried on long erect fertile hyphae, and all that is needed is to pick off a spore or spores on the end of a sterile needle for transferring to a plate of sterile maize-meal agar. A very small block of sterile agar on the end of the needle helps a great deal in making the spores stick. Maize-meal agar is a good medium for pure cultures, and another that I have found useful is Langeron's potato-carrot-agar. Rabbit-dung-agar is another good one, particularly suitable for *Trichothecium flagrans,* which is a difficult species to maintain in pure culture because it so readily loses its power of sporulation. Rich media should not be used for culturing predacious hyphomycetes, and enrichment of media with added carbohydrate should be avoided. Malt agar and, especially, potato-dextrose-agar are, in my opinion, thoroughly bad for predacious fungi.

Pure cultures of predacious hyphomycetes usually do not show the characteristic traps, and to induce trap formation nematodes must be offered to the fungi. This is best done by transferring the fungus to an agar plate already infested with nematodes, rather than by adding nematodes to a flourishing culture of the fungus. One of the major difficulties in working with predacious fungi is maintenance of adequate stocks of eelworms for use when they are required.

<div align="center">CONCLUSION</div>

From the foregoing account it will be seen that our knowledge of the predacious fungi has many gaps. On the morphological side a great deal of work has been done, but their physiology and ecology are virtually unexplored, and many fascinating lines of research are here waiting for investigation. Many taxonomic problems also need clearing up.

The nematode-attacking fungi have a particular economic interest at the present time, for the losses in agricultural produce caused by nematodes are enormous and attempts to control them by chemical means have so far done little more than underline the gravity of the situation. Work already done has suggested that the predacious fungi may be capable of reducing eelworm populations on a useful scale if practical means for their application can be found, but a great deal of investigation is needed before an accurate estimate of their value, if any, can be made. If the predacious fungi are to provide even a partial solution to the eelworm problem, research on a large scale over a period of years will have to be undertaken, needing the financial assistance that only governments can provide. It must be emphasised that their premature use against eelworms in the field is likely to do more harm than good; if success is to be achieved the work must be founded on a knowledge of the ecology and biology of the fungi that can come only from fundamental research.

<div align="center">SUMMARY</div>

The predacious fungi include members of all the Classes but are mainly contained in two groups: the Zoopagaceae and the hyphomycetes. A few have been known for a long time, but most have been discovered during the last two decades. Some predacious fungi were known as " saprophytes " for many years before their true nature was realised. The animals attacked by these

fungi are mostly amoebae and nematode worms, but rotifers and other microscopic animals are also included among their prey. The animals may be trapped by some mechanism such as sticky hyphae or mechanically constricting rings, or there may be adhesive spores that stick to the exterior of the host.

Among the Zoopagaceae, a Family of the Zygomycetes, we find both endozoic and animal-trapping fungi. The endozoic species mainly attack Protozoa, the spores either sticking to the host as it moves about or being ingested. The animal-trapping forms usually consume amoebae, but some of the larger ones capture eelworms which are caught by a sticky secretion of the mycelium. The contents of the captured animal are absorbed by means of haustoria. The Zoopagaceae reproduce asexually by true conidia; where the sexual stage is known, it involves fusion of equal or unequal gametangia.

The *Arthrobotrys* series of predacious hyphomycetes capture their prey, usually nematode worms, by some kind of trap. The traps may be sticky hyphal loops and networks, sticky knobs or branches, hyphal rings into which the eelworms are wedged by their own efforts to pass through, or similar rings in which the cells are sensitive to contact stimuli and are able to swell so as to hold the eelworm by constriction. After the captured animal is dead, its body contents are absorbed by trophic hyphae which fill its carcass.

The endozoic predacious hyphomycetes are parasitic within the bodies of eelworms. The animal is usually infected by means of a sticky spore that becomes attached to its integument. The internal mycelium grows at the expense of the host until the animal is completely filled with hyphae, after which fertile branches from the mycelium pass out through the integument of the dead host into the air and produce their conidia. These endozoic hyphomycetes are taxonomically a mixed group; one genus appears to be an imperfect basidiomycete.

In addition to these two main groups of predacious fungi, others are known. A number of species belong to the Lagenidiales and are parasitic in eelworms. *Zoophagus insidians*, predacious on rotifers, was one of the first predacious fungi to be described; it was placed in the Saprolegniales but may possibly belong to the Zoopagaceae.

The working of the nematode traps of *Arthrobotrys* and its

allies has been investigated by a number of workers. The traps are usually formed only in the presence of eelworms. Sticky traps are adhesive only for eelworms unless they are exposed to dry air, while the constricting ring trap can be sprung by rubbing the inside of the ring with a glass micromanipulator needle. The actual mechanism by which the swelling of the ring is brought about has not been elucidated. In other respects, the physiology of the predacious fungi is almost a closed book.

Little is known about the ecology of predacious fungi. They have been obtained from a variety of sources such as leaf-mould, dung, soil, decaying plant remains, water, rotting wood and living bryophytes, but our knowledge of them is insufficient to allow of any ecological generalisations, and quantitative information is badly needed.

The predacious fungi vary in their degree of host-specificity. The Zoopagaceae that attack Protozoa are usually limited to a single species for prey, but those capturing eelworms are more versatile. The nematode-trapping hyphomycetes usually capture a wide range of species, the limit being mainly one of size, though the structure of the cuticle of the nematode may also be of importance. The endozoic hyphomycetes sometimes show some degree of host-specificity, but are variable in this respect.

The means of dispersal in the predacious fungi is unknown, though it is suggested that their spores might be carried by air currents, small arthropods, earthworms and, in some instances, water. The endozoic hyphomycetes are probably dispersed by their host animals.

Attempts have been made to use the predacious hyphomycetes for the biological control of eelworms. Methods of producing them in quantity have been worked out, and experiments in their actual use have met with a certain amount of success on a small scale. Further work on this may produce interesting results.

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CONTROL OF PLANT DISEASES BY USE OF
ANTAGONISTIC ORGANISMS

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INTRODUCTION

The phenomenon of antagonism between micro-organisms has received much attention during the past few decades. It commonly occurs in plate cultures of pathogens which have become contaminated or in deliberately mixed cultures of pathogens and saprophytes. Many studies have shown that a significant proportion of the organisms found in the environment in which certain diseases develop profoundly affect the growth of the pathogen in pure culture. Inhibition or even complete suppression of growth has often been obtained in these conditions, and indeed in isolated cases active parasitism of the pathogen by a commonly occurring saprophyte has also been reported. The part played by secondary organisms in the development of plant diseases under natural conditions has been increasingly studied. For example, reduction of the severity of certain root diseases by cultural practices, such as green-manuring, has been attributed to changes produced in the nature and activity of the soil micro-flora. Variations in the incidence of disease which are associated with soil differences or seasonal fluctuations in the climate have been similarly explained in some instances. In the light of such evidence it was natural that the use of organisms antagonistic to specific pathogens should be considered as a practical control measure. This review deals with certain aspects of such work and will be confined to diseases caused by fungi; while no attempt has been made to cover the literature completely, it is hoped that no major work has been excluded. No reference will be made to virus diseases, as this would involve a series of special considerations. Neither will the

direct use of specific antibiotics as chemical substances be considered, since the principles governing their use in disease control will probably not differ materially from those applicable to more orthodox fungicides. Antagonism will be interpreted in the widest possible sense to include any activity of one organism which in some way adversely affects another growing in association with it so that the problem of disease control by antagonistic organisms becomes essentially a study of the competition between pathogens and saprophytes and may be approached in the following ways. In the first place, organisms selected for their antagonism to a particular pathogen may be introduced into and maintained in the environment, and so prevent establishment of the pathogen on the host plant or eliminate it as a causal agent. Secondly, conditions within the environment may be altered to produce a similar effect by modifying the nature and activity of the microflora already present. The first approach requires the isolation and selection of appropriate organisms; it is this aspect of the work which will be considered first.

ISOLATION AND SELECTION OF ANTAGONISTS

A series of surveys as well as many isolated reports give information on the types and numbers of organisms antagonistic to particular plant pathogens in pure culture on solid or in liquid media (2–4, 28, 34–36, 39, 110, 115, 119, 133, 138–140, 148, 149). The media used have varied widely in composition; they have usually been those commonly used in mycology laboratories. Antagonistic effects are most readily observed on solid media, and various techniques have been described for their estimation. The majority involve inoculation of the pathogen and test organism on the same plate, followed by observation and measurement of the mutual effects of their growth. Inoculations are generally made so as to permit some growth of the test organism before this is affected by growth of the pathogen. This may be accomplished by inoculating both organisms simultaneously at a distance from each other or by inoculating the test organism some time before the pathogen. The effects of their subsequent growth have been well described by various workers (2–4, 138, 139) and will not be given in detail here. Commonly there is a zone around the antagonist into which the hyphae of the pathogen do not penetrate;

the width of this zone has usually been taken as a measure of the activity of the antagonist. At the edge of such zones various morphogenic effects are frequently seen, distortion or lysis of the hyphae of the pathogen being commonly observed. Behind the edge the hyphae often branch much more profusely than in normal growth and may accumulate to form a distinct ridge, this being sometimes associated with more profuse sporulation. Occasionally isolated hyphae grow into the intervening zone, but with these exceptions the production of a zone means that the growth of both pathogen and antagonist across the surface of the agar sooner or later stops, two distinct colonies being formed.

In other cases no distinct zones are produced; growth of the pathogen stops, its colony then being penetrated and overgrown by hyphae of the antagonist. This is sometimes accompanied by active parasitism of the pathogen. Yet again both antagonist and pathogen may be mutually antagonistic to the extent that linear extension of the colonies takes place until they meet, but no penetration of either colony occurs. An organism showing any of these effects would be potentially useful but in the past attention has been directed to those producing wide zones of inhibition. It is probable, however, that in screening tests with plate cultures a better measure of the antagonistic properties would probably be the extent to which the total growth of the pathogen is inhibited. It is apparent that a slowly growing antagonist may well produce a striking zone of inhibition but competitively may not be so efficient as a very rapidly growing organism which, if its colony is not penetrated by that of the pathogen, limits the latter to a small area, even though the actual zone of inhibition may be absent or very narrow.

Studies such as the above illustrate competition between the antagonist and active hyphae of established colonies of the pathogen. Correlated studies have also been made of the ability of organisms to prevent establishment of a pathogen on an agar surface. This may be done by inoculating a limited area of plates with a suspension of spores or hyphal fragments of the test organism and then adding the pathogen to the same area, immediately or after various intervals. In a modification of this method the antagonist is sown on films of cellophane covering an agar surface. After the antagonist has grown for some time, the

cellophane together with the antagonist is removed and the surface of the agar previously below the colony sown with the pathogen. Curtailment of growth following these treatments is an indication that the pathogen is unable to compete with these organisms or that its growth is adversely affected by one of their metabolic products.

Tests of antagonism in pure culture have generally been made at one temperature only, and this has not always fallen within the range in which the antagonist would be expected to operate naturally. It would seem to be particularly important that a range of temperatures be used in screening tests and that organisms selected for further tests in disease control should have growth-temperature relations similar to those of the pathogen. This is perhaps more important for those diseases able to develop at intermediate or low temperatures, since under normal growing conditions it is unlikely that temperatures high enough to curtail growth of the antagonist would often be experienced.

In most surveys for potential antagonists, media of high nutrient content have been used, the composition probably having little relation to that of the substrate on which antagonistic effects would need to be produced to control disease. Use of such media, whether synthetic or from natural substances, might well give misleading information, since the antagonistic effects in many cases will depend on the production of antibiotic substances, and this is known to be particularly affected by the composition of the medium on which the antagonist is growing. It is always difficult to assess the nutrient conditions under which plant pathogens are active naturally, particularly when dealing with soil or seed-borne diseases. It would, however, always seem desirable to use media as close as possible to the natural substrate in screening tests where the main object is isolation of organisms potentially useful in field conditions. Thus in the case of a soil-borne pathogen a soil extract, and for a plant pathogen a tissue extract of the host, would be more appropriate than a synthetic medium such as Czapek's solution.

Against this view may be put the argument that even in soils the breakdown of fresh plant debris by saprophytes may well lead to a high local concentration of nutrients, even though the general level throughout the soil is quite low.

Some surveys have used liquid in place of solid media. Test organisms have been cultured for a period and removed aseptically. Various dilutions of the culture fluid are then inoculated with the pathogen and the dilution level at which growth is inhibited taken as a measure of the antagonism of the organism. This method has the advantage of precision in operation and of giving a numerical figure of activity but is otherwise less useful for the purpose at present under consideration. In such tests conditions for growth of the antagonist are even further removed from those obtaining naturally than are those of plate culture, particularly when the culture solutions are continuously agitated. Use of these methods is justified only when the main aim is the detection and isolation of antibiotic substances. Their use would not detect, for instance, antagonism by active parasitism of the pathogen or its exclusion by rapid growth of the antagonist.

Tests of antagonism in pure culture are of greatest value when conditions approach, as closely as is practicable, those at the site of the disease. The temperatures for screening tests should fall within the range in which the disease could be expected to develop, and nutrient levels should be those of the natural substrate wherever possible. It is also important that organisms selected for further trial should be types normally occurring in the disease environment and preferably obtained in the first place from it. Selected organisms should of course be non-pathogenic (this rather obvious point has not always been observed) and have properties making them suitable for easy application to plant surfaces or soil, and for rapid establishment. Thus spores or resting bodies should germinate well and quickly, and the organisms should have high growth rates and reproductive capacities, especially of relatively resistant spores. They should be easily cultured on readily available media and be non-exacting in their nutritional requirements; in this way large quantities of inocula could be easily and cheaply prepared.

The results of the many surveys which have been made will not be referred to in detail. It may be stated, however, that in general no difficulty has been experienced in obtaining a large number of species antagonistic to various plant pathogens in pure culture. A good proportion of these occur naturally with the pathogen, and prominent among them are the spore-forming bacteria, actino-

mycetes, species of *Penicillium* and *Trichoderma viride*. This is
to be expected in view of the ubiquity of these organisms and the
frequency with which they are isolated from soil by dilution
methods. In this connection, however, it is to be noted that some
of the species, in particular those of *Penicillium,* may not occur as
actively growing mycelium in soils so frequently as has been sup-
posed, and their importance as antagonists in this medium may well
have been overemphasized. It is also interesting to note that few
of the Phycomycetes, generally considered one of the dominant
groups of soil-inhabiting fungi, exhibit marked antagonism in pure
culture in the narrower sense of producing wide zones of inhibi-
tion. This class includes many rapidly growing species and may
therefore be of considerable importance in the wider competitive
sense under normal soil conditions.

This section concludes on a note of caution. Methods generally
used for isolating organisms from the environment in which disease
is initiated are very selective. This is particularly true for soil
organisms. It may well happen that the methods used fail to
isolate organisms which under natural conditions play an important
part in controlling growth of pathogens. Thus ordinary methods
of isolation from soil rarely produce representatives of the higher
Basidiomycetes, Discomycetes or Pyrenomycetes. There is no easy
solution to this particular problem. New methods of isolation
are required which give a more balanced picture of the soil micro-
flora as it occurs naturally.

DISEASE CONTROL—GENERAL CONSIDERATIONS

Where direct use of antagonists is envisaged, isolation and selec-
tion of organisms have generally been followed by an investigation
of their ability to control disease in the absence of competition
from organisms other than the pathogen. The methods which
have been used necessarily vary with the type of disease under
study. Much of the work along these lines has been done with
soil-borne diseases, and here the technique has been to sterilize the
soil, to inoculate it with the antagonist either simultaneously or
some time before the pathogen, and after suitable intervals to test
for the presence of the pathogen by growing susceptible hosts in it.
With pathogens affecting aerial parts of plants, the plant tissue
has been surface sterilized, damaged in some way when the

pathogen is a wound parasite, and inoculated with the pathogen simultaneously or after earlier inoculation with the antagonist. Under such conditions, control of disease has been obtained in a considerable number of cases and might well have been anticipated for organisms antagonistic under the conditions outlined in the previous section.   Such experiments are in effect studies of antagonism in pure culture using natural substrates.   They are of value in demonstrating that the selected antagonists are able or unable to grow and act antagonistically under such conditions and that their activity was not dependent upon the even more abnormal conditions of Petri dish or flask culture.   The final stage is reached when organisms are tested for their ability to control disease under natural conditions and therefore in the presence of the normal microflora.   Complications now arise, owing to the introduction into the disease complex of a variable factor, the importance of which is assessed only with difficulty, viz., competition between the antagonist and the saprophytes commonly associated with the pathogen.   When disease does develop, the pathogen has obviously survived similar competition; the frequent inability of the introduced antagonist to become established and to multiply in the face of this competition probably accounts for the fact that there are few reports of disease control under these conditions and that conflicting results have been reported for similar experiments, even by the same worker.   Nevertheless this is the stage of greatest importance; earlier ones can be regarded as essential preliminaries in all but a small minority of diseases.

Indirect use of antagonists is suggested by the fact that in many cases the microflora normally associated with the pathogen includes a number highly antagonistic in pure culture.   Furthermore, certain treatments leading to a reduction in the incidence of disease have been shown to produce, at the same time, changes in the number and composition of this microflora.   Indeed, it seems likely that some natural fluctuations in disease are caused by environmental variations affecting the pathogen not directly but indirectly by changing the activity of this microflora.   Precise analysis of such changes presents great difficulties; it is only within broad limits that the effect of particular treatments or conditions can be predicted.   It was therefore inevitable that the approach to this aspect of disease control has been largely em-

pirical and indeed is likely to remain so for some time in the future. Nevertheless, some encouraging results have already been obtained.

An account now follows of the work done in this field by the direct or indirect use of antagonists. No attempt will be made to consider the various diseases on a taxonomic basis; they will be dealt with in the first place in arbitrary groups, but subsequently the general problems involved in diseases of aerial parts of the plant, on the one hand, and of subterranean parts, on the other, will be discussed separately.

CONTROL OF SPECIFIC DISEASES

POTATO SCAB CAUSED BY *Actinomyces* (*Streptomyces*) *scabies.* This was the subject of one of the earliest comprehensive investigations of disease control by microbiological methods and is one of the few diseases for which some success has been reported under field conditions. It was shown (122, 123) that application of green manure to heavily infested soil gave substantial control of scab and also partially offset the increased severity of disease which generally followed heavy applications of lime. A series of pot experiments demonstrated that addition of green manure to sterile soil heavily infested with the pathogen was ineffective but that simultaneous addition of a saprophytic actinomycete, *Actinomyces praecox,* gave substantial control of the disease. This was associated with an almost complete suppression of the pathogen in the early stages of the experiment and a very considerable reduction later on. The control exercised by the addition of green manure was attributed to the fact that soils in which scab normally develops are generally low in organic matter; addition of a readily available organic food material might be expected, therefore, to lead to an increased growth of both saprophytic and parasitic actinomycetes. It was then postulated that under such conditions obligate saprophytes became dominant and, by appropriation of the available food supply and secretion of toxins, prevented multiplication of or even eliminated the parasitic types.

The failure of green manuring to control scab in a Canadian soil was attributed to the low pH (5.0–5.4) of this soil and the possibility that suitable antagonistic actinomycetes were either absent from this soil or were unable to multiply under acid conditions (147).

Work along similar lines has demonstrated control of this disease in sterile soil by the addition of an extract of unsterilized soil or manure, but, in contrast, addition of certain penicillia, bacteria or actinomycetes, including *A. praecox,* had no effect. In the field the addition of unsterile or sterile manure reduced scab; green manure was, however, ineffective (63).

Yet another antagonist has been studied in this respect. A species of *Trichoderma* was shown to be antagonistic to the pathogen in pure culture and also to give some reduction of disease when added as a suspension in furrows about the developing tubers (38). Further work on the effect of green manuring has shown in pot experiments with naturally infested soil that addition of two successive six-week-old crops of soy-bean reduced the percentage of the tuber surface covered by lesions from 48.1 to 10.3. Similar treatment with rye or clover, however, had little effect. Parallel studies on the effect of these treatments on the soil microflora showed that addition of rye had no appreciable effect on the number of fungi or actinomycetes but increased the bacterial population. Clover and soy-bean both caused large increases in all three groups, soy-bean being particularly effective in increasing the fungal population. It was also the only one to lower the pH significantly, reducing it from 6.4 to 5.0 (11, 145).

Some conflicting results have therefore been reported for this disease. While there is a measure of agreement that certain types of manuring are followed by a reduction in the incidence of the disease and that this reduction is attributable to a direct effect of the amendment on the numbers and activity of the soil microflora, there is no unanimity as to the group of organisms primarily concerned. Here may be quoted the results of recent work which demonstrated a wide range of cross-antagonisms among actinomycetes which were all antagonistic to *Streptomyces scabies,* making it unlikely that any one type would become dominant in a mixed population (108). The actual mechanism of the control which has been reported by such simple cultural methods has therefore still to be elucidated. It may well be different with different soils and climatic conditions.

DISEASES CAUSED BY *Rhizoctonia solani.* Investigation of this group of diseases was stimulated by the discovery of the active parasitism of the pathogen by *Trichoderma viride* in pure culture and that this fungus secreted into liquid media a substance later

identified as gliotoxin, highly toxic to this and other organisms in high dilution (177–180). The ability of this antagonist to control damping-off of citrus seedlings has been extensively studied. In a series of pot experiments the bottom layer of soil was inoculated with the pathogen and overlaid by peat in which were sown seeds of citrus plants. Addition of a suspension of spores of *T. viride* to the peat layer was effective in controlling damping-off when the pH was lower than 4.5, less effective at pH 5.7–6.1 and ineffective at pH 7.0. Addition of sand or soil to the peat layer also reduced the efficacy of this treatment. Control of disease affecting six- to eight-week-old seedlings was also obtained when the pathogen was added to the sub-soil and the upper layer of soil replaced with peat containing the antagonist or with soil acidified to pH 4.9. When seed was sown in soil at different pH values there was complete loss of seedlings at pH 7.3, partial control of damping-off at pH 4.9 and complete control at pH 4.0. Addition of the antagonist to soil at pH 6.4 to 6.7 or sand at pH 7.3 to 7.8 was quite ineffective. A parallel series of seed-bed experiments substantially confirmed these results. Here there was a considerable reduction in the area of seed-beds with damped-off seedlings after acidifying the upper layer of the soil or sowing the seed between layers of peat inoculated with the antagonist (181). These findings with acidified soil confirmed earlier work in which a series of soil treatments were tested for their ability to reduce losses of conifer seedlings caused by a number of pathogens, of which *R. solani* was one of the most important. Acidification of the seed-bed soil with aluminum sulphate or sulphuric acid was among the most effective and persistent treatments, and its practical use was recommended (169, 183). While the part played by micro-organisms in this acid treatment is by no means certain, that it is of some significance is suggested by the fact that *T. viride* is commonly found in such soil and that gliotoxin, one of the potent antibiotics secreted by this fungus, is stable only in relatively acid solutions. However, while this fungus produces gliotoxin in sterile soil, this material can not be detected in unsterile soil, even with very sensitive methods of assay (51).

A number of later investigations have emphasized the interaction between the soil microflora and this pathogen, and in particular have dealt with the activity of *T. viride* or related forms.

Cultures of this fungus grown on sterilized soil and added to sterile or unsterile potting soil which had been inoculated with the pathogen produced significant reductions of the numbers of diseased pea or cucumber seedlings (5, 70). Further experiments with a strain of *Bacillus simplex* which was active against the pathogen in vitro also produced similar results. In these tests increased stands of seedlings were obtained by adding to greenhouse soil (presumably unsterile) containing the pathogen, a water suspension of the bacteria or autoclaved broth cultures. It is to be noted, however, that equally significant results were obtained when an uninoculated medium was added (37). In another extensive series of studies with this pathogen, a special point was made of working under sterile conditions, thus avoiding many of the uncertainties which are inevitable when organisms are introduced into unsterile soil. Sterile seedlings of the Chinese cabbage were raised in culture tubes sealed with cotton wool. These were inoculated with the pathogen and one or more of a number of antagonists. The strongest antagonism was produced by two strains of *Trichoderma lignorum* followed by *Pyronema confluens, Cylindrocarpon didymum, Penicillium expansum, Cladosporium herbarum* and *Absidia spinosa.* The effect of more than one antagonist was additive except with *C. didymum* which reduced the antagonism of others. Generally similar results were obtained in pot experiments (79). In comparable work with lettuce seedlings, using sterilized sand or soil inoculated with the pathogen, almost complete control of disease was obtained by adding in a variety of ways organisms selected for their antagonism on a soil-extract agar. Those used included *T. viride, Penicillium clavariaeforme* and various species of actinomycetes and sporeforming bacteria. Parallel experiments with unsterile soil produced quite different results. Although the majority of organisms tested were somewhat effective in the early stages, this result did not persist, although two of the antagonists could be seen growing freely in the soil interstices (187).

An investigation of the black-root disease of beet led to the isolation of a number of strains of this pathogen and also to that of a new species, *Papulospora stoveri,* which was shown to be parasitic on the pathogen in pure culture. Addition of cultures of this antagonist to infested soil led to increased stands of seedlings

in two of three sowings over a period of 55 days (176). This disease was also controlled in sterile soil by pre-inoculation with a strain of *Bacillus subtilis* (46).

Other investigations have dealt with the effect of soil amendments on this pathogen with and without further addition of antagonists. Thus in one series of experiments an amendment of dried grass in unsterile soil caused a very significant reduction of disease of lettuce seedlings which was not increased by further addition of antagonists. Maize meal, however, was effective only after inoculation with antagonists (187). Similarly, with radish seedlings reduction of disease was obtained with a variety of organic amendments in a number of soil-types. This control was associated with a profuse development of other micro-organisms and was not observed in sterile soil. The effect of adding groups of these antagonists with and without organic supplements was also studied. In sterile soil the supplements alone did not reduce disease, but they did give some, though not much, control in the presence of the antagonists. In unsterile soil, substantial reduction of disease was obtained by the amendments; this was not further increased by adding antagonists. The positive results were attributed to an increase in the activity of the soil micro-flora able to utilize the amendments, leading to a nitrogen starvation of the mycelium of the pathogen and inhibition of its growth by an increase in the concentration of carbon dioxide in the soil (17, 18).

A comprehensive series of experiments extending over eight years has dealt with the effects of a variety of inorganic and organic amendments on the severity with which sprouts of potato tubers are attacked by this pathogen. The treatments were applied to unsterile soil inoculated under natural conditions in a standard manner with cultures of the fungus grown on sterile soil. A feature of the results obtained was the wide variation in the amount of disease recorded for replicates of the same planting and between corresponding replicates of different plantings. In view of this the results are not easy to summarize, but in general terms it may be said that nitrogenous salts and maize meal caused the most significant reduction of disease and that sucrose, lime, sulphur and magnesium sulphate increased the virulence and persistence of the pathogen. The basis of these differences was not established but they were not connected with pH changes; while the addition of

maize meal caused profuse fungal growth, this did not occur with the nitrogen salts (151, 152). In a continuation of this work it was shown that the pathogen disappeared from natural soil within 120 days in the absence of a suitable host, in this case potato plants. In the presence of the host plants, the pathogen persisted as well in untreated soil as in soils supplemented with maize meal, sodium nitrate or calcium hydroxide (153).

There seems to have been little work done on the extension to the field of results obtained in pot experiments. In one such series of experiments in naturally infested soil no positive results were obtained by addition of cultures of antagonists to lettuce seed-beds, although the organisms used were highly active in vitro and one had been selected for its ability to grow and act antagonistically at low temperatures. However, certain other treatments under the same conditions did succeed in significantly increasing the stand of plants in winter seed-beds. There was again in this work a wide variation between replicates of different treatments. Three of these, application of green manure or maize meal or keeping the soil wet some months before sowing, reduced the incidence of damping-off. Rather surprisingly, plots in which the upper layer of soil had been kept dry throughout the summer produced considerably fewer seedlings than those which were untreated. These results confirmed field observations that damping-off in winter seed-beds was generally more severe following a warm dry summer (187).

The general conclusions from the above investigations are that many soil organisms are antagonistic to this pathogen, some indeed actually parasitic, and that certain are able to control disease in soil in the absence of other saprophytes. Less frequently, similar control has been obtained in pot experiments with unsterile soil. Further application of these methods under field conditions seems to have been attempted in relatively few cases and then with negative or uncertain results. More promising as a practical measure is the use of soil amendments. Here, as good or better results have been obtained than by use of the most potent antagonists selected by pure culture screening tests. A point in favor of such methods is of course that they are effective only in unsterile soil and compared with any addition of fungal or bacterial inocula, would be relatively cheap. However, even with

these treatments under field conditions erratic results have been obtained. Since variation *in disease occurs naturally between different soils and at different times, some natural biological control of the pathogen is indicated.* It is important to note here that conditions favorable for vegetative growth of the pathogen sometimes depresses its virulence and that virulence is often greater in natural than in sterilized soil (150). A profitable approach to the control of diseases caused by this and other soil-borne fungi might be to analyze the conditions under which the pathogen disappears from the soil or becomes virulent in order to provide data on which to base the development of special cultural operations aimed at creating these conditions artificially.

DISEASES CAUSED BY *Phytophthora and Pythium* spp. These diseases rather closely resemble in their development those caused by *Rhizoctonia solani,* and in general the studies made with them and the results obtained have been similar. An early investigation dealt with the damping-off of seedlings in forest nurseries caused by *Pythium debaryanum.* Sterilized soil in pots was inoculated with the pathogen and then with cultures of a variety of organisms, including *Trichoderma koningi, Phoma* spp., *Chaetomium* sp., *Rhizopus nigricans, Trichothecium roseum, Aspergillus* spp., *Penicillium* spp., *Bacterium* sp. and unidentified fungi. Pots inoculated with the saprophytes gave increased emergence and increased final stand. Application of the saprophytes to seed-beds was, however, ineffective (72).

Damping-off of tomato seedlings by *Phytophthora parasitica* and *P. cryptogea* and its control by microbiological methods have been the subjects of an extensive series of investigations containing much information on the formation of antibiotics by selected antagonists in soil amended in various ways (68, 69). These aspects of the problem will not be described here, but the implications of this and similar work will be referred to later. It will be noted, however, that in these experiments some control of disease was obtained in sterile soil by the addition of cultures of *Aspergillus clavatus* or *Penicillium clavatum* on suitable organic media. Here the technique was to incubate the soils after addition of the antagonists and then to inoculate with the pathogen. Control was substantially increased when, in addition, the soil was sprayed with a glucose solution (68, 69). In greenhouse tests with *P. parasitica*

inoculation of the soil of pots or of hotbeds with *T. koningi* led to increased stands of seedlings. In two such experiments under these conditions increases from 207 to 557 and from 98 to 287 compared with total stands of just over 800 in the untreated plots were obtained (90). Results of the work with *Pythium* spp. parasitizing various grasses or lucerne conform to the same general pattern, a wide range of organisms and a soil suspension increasing the number of healthy seedlings grown in sterile conditions in tubes. In this work it was shown, too, that weak or non-pathogenic species of *Pythium* also acted as antagonists to virulent strains and led to a reduction of disease caused by them (110). This effect was also observed with isolates from strawberry plants affected with root-rot (136).

A survey of the actinomycetes isolated from certain Iowa soils showed that 21 per cent were antagonistic to *Pythium graminicola* which causes a root-rot of corn plants. Addition of crude culture filtrates of one of the most antagonistic of the isolates to soil infested with the pathogen increased both the height and root systems of corn plants (121).

The influence of the soil microflora on the development of root-rot in sugar cane and corn caused by *Pythium arrhenomanes* has been very extensively studied, particularly in recent years. An earlier investigation had shown that a number of actinomycetes from sugar cane soils were strikingly antagonistic to the pathogen in pure culture. Root-rot of both cane and corn was reduced in sterile soil by adding a culture of one of the most active forms (168). Later, extensive surveys of the actinomycete, bacterial and fungal flora of a variety of soil types in Louisiana was undertaken (34–36, 111, 112). At intervals throughout the year, thousands of isolates from these major groups were tested in plate culture for their antagonism to this pathogen, and an attempt was made to estimate the microbiological activity of a soil against *P. arrhenomanes* by calculating first the " Antibiotic Index ", this being the average distance in millimeters of the inhibition zone between the various isolates and the pathogen on agar plates, and then the " Antibiotic Value " which is the Antibiotic Index × number of organisms per gram of soil.

The percentage of actinomycete isolates showing antagonism varied from 18.5 to 31.5 in different soils, the average inhibitory

activity increasing with soil pH, although this factor did not in-
crease the size of the actinomycete population.   It was shown,
however, that the population of antibiotic forms was higher in the
heavy soils generally favoring the disease and lower in the lighter
soils where disease was normally less severe (34, 35).   Similar
results were obtained from analysis of the fungal population of
heavy clay and light sandy soils, the antibiotic values being higher
in the former.   Approximately 15 per cent of the isolates tested
were antagonistic in pure culture, the majority occurring in the
genera *Penicillium, Aspergillus* and *Spicaria* (111, 112).   Con-
siderably lower values were obtained for the 5,638 bacterial isolates
tested, only some 3.6 per cent on a sample basis showing an-
tagonism (36).

While these studies have contributed much information on the
activity of the microflora in different soils and at different seasons
and have shown that relatively high proportions of isolates from
these floras are antagonistic to this pathogen, so far no correlation
between the antibiotic activity of different soils and the prev-
alence of root-rot has been demonstrated.   More promising re-
sults were obtained with certain experiments under controlled
conditions.   Here, autoclaved soil artificially infested with *P.
arrhenomanes* was exposed to the atmosphere.   The populations
of fungi, actinomycetes and bacteria on recolonization were as-
sessed by dilution methods and the disease potential of the soil
by measurement of the amount of root-rot of corn plants.   No
correlation was found between the Antibiotic Index for any of the
groups of organisms and the amount of root-rot, but a definite
relation was revealed between the Antibiotic Value of the actino-
mycete population and the amount of root damage.   The effect of
selected fungal and actinomycete antagonists in reducing disease
in sterile soil subsequently infested with the pathogen was also
studied.   While some forms which were highly antagonistic in
pure culture gave control of root-rot in these tests, others were
quite ineffective.   It can fairly safely be assumed that a larger
proportion still of such forms showing in vitro activity would have
no effect on the disease when introduced into unsterile soil
directly as cultures (83–86).   This difficulty of extending results
obtained in pure culture or sterile soil to unsterile soil is well
illustrated in recent work on the control of damping-off of alfalfa

caused by *P. debaryanum* and *P. ultimum*. In sterile loam both *T. lignorum* and *Streptomyces* sp. gave good control of disease when the soil was amended with 1% glucose. Similarly, good results were obtained when seed pelleted with *T. lignorum* was used. No control was obtained, however, when this antagonist was added to natural soil artificially or naturally infested with the pathogens. More promising results were obtained in unsterile soil amended with 1% ground oat-straw when one of a number of antagonists was added to the covering soil. At high greenhouse temperatures there was practically no damping-off, but at lower temperatures, although a similar protection was obtained in the early stages, the effect was only temporary, the treatment finally being ineffective (67).

In concluding this section mention must be made of the reports of active parasitism of certain pythiaceous root-rotting fungi by a variety of soil organisms, including other species of the genus *Pythium* (42–45). The possible significance of such parasitism in the natural fluctuation of populations of these pathogens, both in different soils and at different times, has been pointed out; the real importance has still to be assessed.

COTTON ROOT-ROT. The sequence of studies with this disease caused by *Phymatotrichum omnivorum* has been rather different from those made with other soil fungi. The efficacy of certain cultural treatments in reducing disease was first established by ad hoc methods and only subsequently were the mechanisms of the control investigated. An early report stated that addition of stable manure reduced the disease in infested fields (135). This and further investigations of the disease in Arizona showed that over many years substantial control had been obtained by applying organic manures along deep furrows during the fall and winter months. A definite reduction of disease followed the first application to infested soil, and in succeeding years the disease was never severe on plots treated in this way (95–97). These results were obtained within the irrigated zone; the method was not so successful elsewhere (157, 165). Analysis of the microbiological activity of treated and untreated soils showed that plots manured over periods of ten to twelve years had a considerably higher carbon dioxide output, higher numbers of bacteria, actinomycetes and

fungi, and a lower infestation by the pathogen than had untreated plots. The pathogen was, however, still relatively abundant in the manured plots. It was thought unlikely that the activity of the larger microbial population would produce carbon dioxide at rates high enough to build up concentrations inhibitory to the growth of the pathogen. As an alternative explanation an increased production of antibiotic substances under the conditions of heavy manuring was proposed (96). In further work on the seasonal fluctuations in the soil flora and the effects of ploughing in crops of sorghum or cowpea, it was found that a sharp increase in the population of bacteria, actinomycetes and fungi generally occurred early in the year. This was followed in the succeeding months by a fall in number which was continuous except for actinomycetes where a second but smaller increase occurred in November. The treatments had no great effect on the fungal population but gave very large increases in the bacterial and actinomycete populations (124). Detailed studies on the effect of similar treatments on the pathogen itself showed that, while it developed quickly and persisted for 16 days in untreated soil, in soil to which three per cent barnyard manure or chopped sorghum was added, it either failed to grow or the limited growth which did occur quickly disintegrated. Cotton seed meal, chopped hulls or cotton roots behaved similarly. In laboratory experiments on the survival of sclerotia, 19.6 per cent were eliminated in unamended soils, corresponding figures of 64.9 and 69.7 being obtained when barnyard manure and sorghum, respectively, were added. The major reduction in numbers occurred during the period of greatest microbiological activity following the addition of the amendments (125). In experiments on a field scale a substantial reduction in the number of diseased plants in infested fields was obtained by incorporating the amendments into soil by deep rotary ploughing (88, 89, 125). Similar effects have been produced by ploughing in cover crops of various legumes (113, 144).

In parallel work on the persistence of sclerotia, no difference in the survival rate was found in amended or untreated sterilized soils. In unsterilized soils, however, it was found that incubation temperatures favoring general microbial activity caused greatest loss of viability of sclerotia; 12, 32, 72 and 90 per cent of these were destroyed at soil temperatures of 2, 12, 28 and 35° C., while

soil moisture contents were found effective in the order 35, 58 and 80 per cent of water-holding capacity (32, 33).

These and similar results leave little doubt as to the efficiency of organic amendments in reducing losses caused by this pathogen, and indeed substantial results have been obtained on a field scale. Although there is a certain amount of circumstantial evidence that the activity of the soil microflora plays a part in this control, no direct proof is yet available and will be very difficult to obtain. It is known, however, that treatments which altered the carbohydrate content of the root bark of plants of fruiting age and which had a marked influence on the susceptibility of the plants to attack were also associated with marked changes in the bacterial flora at the root surface. High carbohydrate levels which increased the resistance of the plants also led to increased numbers of blue-green fluorescent bacteria. At the same time, however, there was a reduction in the total number of bacteria. Additional evidence that microbiological factors are involved was provided by the observation that maize plants, normally highly resistant to this pathogen, were severely attacked when grown in an infested sand and bentonite mixture previously sterilized, while in untreated soil, plants were unaffected, although strands of the pathogen could be seen growing in close proximity to the roots of the host. The nature and activity of the microflora at the root surface was therefore considered to be important in determining whether or not an attack of the roots by the pathogen developed (47). In this connection it is interesting to note that it has been found possible to modify this flora by direct inoculation. The organisms, *Aspergillus luchiensis, Penicillium luteum* and *T. lignorum,* antagonistic to the pathogen in pure culture, became established and multiplied in the rhizosphere of cotton roots after introduction either by seed inoculation or by direct addition to exposed root crowns. In each case the above organisms were recovered at considerable distances from the point of introduction in considerably greater numbers than in the control series (127). The direct parasitism of hyphae of the pathogen by the common saphrophyte *T. lignorum* has also been demonstrated (26, 27).

While much work remains to be done to elucidate the microbiological aspects of the effect of organic amendments and the factors involved in the comparative failure of these treatments in

certain areas, the successful control by such cultural methods in irrigated soils is particularly encouraging when one considers the very wide host-range of this pathogen and the absence of alternative methods.

CEREAL DISEASES CAUSED BY *Ophiobolus graminis, Fusarium* spp. AND *Helminthosporium* spp. The occurrence and development of diseases in relation to the activity of an associated microflora have probably been more extensively studied for this than for any other group of diseases. Particularly prominent is the work which has been done in Canada where the complex of diseases caused by these pathogens is of major importance. Infection of young seedlings arises either from soil-borne mycelium which may be closely associated with crop residues or from fungal material carried in or on the seed. The work which has been done on the microbiological control of these diseases may be conveniently grouped on this basis, and in this section the influence of the soil microflora on the survival and activity of the pathogens in soil will be considered. In this respect the studies with *O. graminis* are probably the most extensive and significant. No difficulty has been experienced in isolating from soils a wide variety of organisms antagonistic in pure culture to this fungus, and a considerable number of experiments have shown that, while inocula of the pathogen retain full virulence in sterile soil, their pathogenicity is reduced or even lost in unsterile soil (24, 54, 55, 109, 126, 134, 148, 151, 158, 184, 185). This is particularly marked under conditions which might be expected to favor a high level of microbial activity, e.g., high temperatures and relatively high soil moistures (56, 74). Similarly it has been repeatedly shown that a wide variety of organisms is able to give some control of disease in soil previously sterilized, but the results obtained under such conditions are poorly correlated with expectations based on observations of antagonism in pure culture (24, 102, 148, 160). Thus in one series of experiments of 45 organisms more or less ineffective in sterilized soil, 28 showed considerable antagonism to the pathogen on nutrient agar. In contrast, one species, *Typhula graminum,* which gave moderate control in soil and showed some antagonism on one type of agar, was compatible with the fungus on another (24). A decrease in virulence in sterilized soil has been observed generally when this is allowed to be recolonized by a saprophytic

flora; indeed it has been shown that in sterilized soil there may be a greater suppression of the pathogen than in natural soil, indicating that the original flora has been replaced, perhaps temporarily, by one more antagonistic (109).

Evidence that microbiological activity may be of importance under natural conditions is provided by experiments in which the severity of the disease was investigated in sterile and unsterile soil artificially infested and held at various temperatures. There was little difference at 13° and 18° C., but at higher temperatures the virulence of the pathogen was much reduced in the unsterile but not in the sterile series. This effect was attributed to increased activity of the soil microflora at the higher temperatures (74). However, alternative explanations of similar results in other experiments have been proposed. Thus in an investigation of the effect of organic amendments in natural soil, no correlation was found between the amount by which disease was reduced and the bacterial populations when these were estimated over the succeeding seven weeks (32). With this may be associated the observation that there were no major differences in the kind and number of microorganisms in naturally infested and clean prairie soils (32) and that while manuring may induce large increases in the microbial population of the soil generally, similar effects were not produced in the microflora of the root surface (31). Amendments reducing disease did, however, produce relatively large increases in the amounts of available phosphorus and nitrate nitrogen. Furthermore, the onset of disease in treated soils coincided with the disappearance of nitrate nitrogen from the soil (32). In further studies along these lines no correlation could be demonstrated between the severity of disease and the level of available phosphorus in infested and clean prairie soils, but it was shown in pot experiments with infested soil that the disease could be checked if superphosphate were added at planting time and a high level of nitrogen maintained throughout the growing season by repeated application of small quantities. The failure of other greenhouse experiments to demonstrate control by addition of inorganic materials was attributed to the fact that the amounts normally applied were considerably below those which would be available to individual wheat plants in heavily manured fields. This work therefore stresses the beneficial effect of certain organic and in-

organic additions to infested soil, and, while not discounting the part played by the microflora in indirectly influencing the activity of the pathogen, the results suggest that the principal effects of these treatments is to produce through the increased availability of essential nutrients plants less susceptible to attack (164). The results of another series of investigations on the effect of soil conditions on the development of this desease have suggested two further hypotheses to explain the way in which these and other soil amendments act and also the action of certain other factors known to influence attack of the host plant. The pathogen is considered in the first place to spread through the soil only on the roots of host plants and there to have an ascendant parasitic phase which is followed later by a pseudosaprophytic phase in which it persists on dead host tissue. Studies were made of the rate at which hyphae of the pathogen grew along the roots of wheat plants under a wide variety of soil conditions. The treatments tested included different soil types, soils at different pH values and moisture contents, soils sterilized by steam or various chemicals and soil artificially aerated. From the results obtained and from field observations on the occurrence of the disease it was suggested that the main factor retarding the growth of the pathogen along the roots of host plants was its susceptibility to high concentrations of carbon dioxide. Soil conditions favoring high carbon dioxide formation or low absorption would therefore adversely affect the pathogen and give a reduction of disease. They would include stimulation of microbial activity by addition of relatively large quantities of readily available organic amendments or suitable inorganic fertilizers (57, 58). In the saprophytic phase other factors were considered of importance. It was shown that the loss of viability of the fungus after it had colonized stubble was hastened by the addition of certain materials rich in carbohydrate but poor in nitrogen, e.g., starch or rye-grass meal, but was delayed by adding dried blood containing 13 per cent nitrogen, although this was followed by a more rapid decomposition of the straw. It was also shown that assimilable nitrogen prolonged the life of the fungus on the straw when added to the straw itself or to the surrounding soil (59, 60). Under field conditions the disease rating was reduced by growing an undersown trefoil crop on the stubble of the autumn crop and ploughing in this crop the following spring.

In this case the effect was, in part at least, thought to be produced by competition for available nitrogen between the crop and the pathogen (60).

No clear picture emerges from the very considerable work which has been done with this pathogen. It is clear, however, that the virulence and survival of the fungus are particularly sensitive to soil conditions and that a large measure of control may be obtained in the field by relatively simple cultural operations. The importance of the soil microflora in these experiments is, however, still a matter for conjecture; much of the effect obtained may depend on alterations in the susceptibility of the host to attack and on its ability to counter attacks of the pathogen by producing new roots under suitable nutrient conditions (7). In considering the persistence of the fungus in the absence of the host, such considerations do not apply and here microbiological factors are obviously at work; various mechanisms of control have been suggested and it is quite possible that several are involved under natural conditions.

Very similar work has been done with the other fungi associated with the " foot-rot " complex, particularly with *F. culmorum* and *H. sativum*. Again, the soil has been shown to contain a large number of organisms antagonistic to the pathogens in pure culture, some of which also gave a good measure of control when added to infested soil previously sterilized (8, 16, 66, 87, 91, 99, 103, 149, 151, 161). The influence of one pathogen in reducing infection by another has also been demonstrated (6, 104). Inocula of *H. sativum* and *F. culmorum* added to sterile soil and tested by sowing wheat seed at ten-day intervals gradually lose their virulence, the reduction being most marked in the first 40 days. In unsterilized soil virulence is much less than in sterilized soil, and here, too, it rapidly declines, being almost lost after ten days (23). The susceptibility of *H. sativum* to soil saprophytes was further shown by the failure of the pathogen to colonize unsterilized wheat stubble, although it grew readily on this substrate after sterilization. Similarly its growth was inhibited on green cuims which had been moistened and incubated, although it grew and sporulated on culms before this treatment (159). Relatively little work has been done with these pathogens in natural soil; this is understandable in view of the difficulty generally experienced in establishing them under

these conditions. However, one such series has included experiments with natural soil. In preliminary pot trials one pint of an oat and wheat inoculum of an antagonist was added to four six-inch pots of sterilized soil. Infestation by the pathogen, *H. sativum,* was at a similar rate. In the field one pint of an inoculum of the antagonist was mixed with one pint of a culture of the pathogen and the mixture distributed along an 18-foot row. Substantial reduction of disease was obtained in both series of experiments by using separately, each of the following antagonists, *B. subtilis, T. viride* and *Penicillium* sp. It should be noted, however, that particularly large amounts of the antagonists were used in the pot tests and that in the field the method of inoculation established an association between pathogen and antagonist much more intimate than would have been obtained had the antagonist been added directly to infested soil in its natural state (8).

No comprehensive surveys on the effects of soil amendments on the virulence and persistence of these pathogens seem to have been made. The influence of micro-organisms on the seed-borne phases of diseases caused by these organisms will be considered in the following section.

SEED-BORNE DISEASES. Most of the work to be considered in this section relates to the seed-borne phases of attack of cereals by species of *Fusarium* and *Helminthosporium*. Other seed-borne diseases will also be included in this section, since the general problems involved for all are the same. *Prima facie,* this group of diseases would be considered the one most amenable to control by antagonists, especially in those cases where the pathogen is carried superficially, since no great problem would be involved in applying relatively large quantities of the antagonists to the limited area in which the pathogen is concentrated and from which it must grow. Some success along these lines has in fact been reported; either antagonists have been introduced into the local environment about the seed or use has been made of the saprophytic flora already present in a dormant state on most seed used commercially. Russian workers have been active in this field and have shown that inoculation of flax seed carrying the pathogens *Fusarium lini* or *Colletotrichum linicola* with certain soil bacteria capable of lysing these fungi, caused an increase in the number of healthy seedlings of certain varieties, although not of others (132). In

similar experiments with wheat artificially infested with *F. graminearum* large increases in the yield of grain were obtained when suspensions of a mycolytic bacterium or filtrates from liquid cultures of it were added to the suspension of the pathogen used for contaminating the seed before sowing (93, 94). Further experiments with flax wilt showed that treatment of seed with mycolytic bacteria produced a ten per cent increase in germinability, a 15 per cent reduction in the incidence of wilt at harvest and a ten per cent increase in yield. Similarly seed treatment of wheat with isolates of *Pseudomonas* or *Achromobacter* increased the percentage of healthy seedlings from 87 to 93 in clean samples and from 41 to 48 in samples infested with *Fusarium*. Corresponding increases in grain yield of some 30 per cent were obtained in pot trials (15). Damping-off of seedlings of *Pinus sylvestris* caused by seed or soil-borne species of *Fusarium* has also been controlled by treating the seed with a suspension of bacteria known from pure culture studies to cause relatively rapid lysis of the hyphae of the pathogen. Isolates of the genera *Pseudomonas* and *Achromobacter* were the most effective and under selected conditions reduced the amount of disease by 70 to 90 per cent (100). The results obtained in rather similar studies with barley seed naturally infested with *Fusarium* spp. and *Helminthosporium* sp. were less conclusive. A variety of organisms isolated from diseased barley seed or from soil continuously cropped with barley for 15 years were tested for their ability to reduce disease by these pathogens under a variety of conditions, e.g., treatments of seed with suspensions of spores and mycelial fragments of antagonists before sowing in the field, applying large quantities of cultures of antagonists to soil in the field or to sterilized sand in the green-house. Infected seed was also soaked in cultures of certain saprophytes for four hours before sowing, and with this treatment some reduction of disease was produced by cultures of *A. scabies* and *T. lignorum* used on seed infected with *Fusarium* spp. The other treatments were, however, largely ineffective. At least one of the antagonists used, *T. lignorum,* was antagonistic to *H. sativum*. Similar results were obtained when clean seed was superficially contaminated with a spore suspension of this pathogen and certain other saprophytes, and then sown in sterilized soil. A bacterium and also *Chaetomium spirochaete* re-

duced the number of deformed or stunted seedlings under these conditions.   It was concluded from this work that the soil microflora did not have a marked effect on the incidence of seedling blight arising from barley seed infected with these pathogens; indeed it was noted that there were no differences in germination and amount of seedling injury when infected seed was planted in sterilized or unsterilized soil (30).   In some contrast to these conclusions are those from work in which the influence of the saprophytic flora on the seed surface has been studied in relation to seedling blight caused by *H. sativum*.   Here it was found that wheat seed incubated in a moist chamber for 24 hours before inoculation with the pathogen produced fewer diseased seedlings than a non-incubated series.   A similar reduction was obtained when the seed was first soaked in a suspension of an antagonistic bacterium.   These tests were carried out on the surface of blotting-paper in test tubes so that neither pathogen nor saprophyte was subjected to the competition of the soil flora (159).   Complementary effects were produced when seed was treated with formaldehyde and lactic acid which almost completely removed the bacterial flora of the seed.   Subsequent inoculation with *H. sativum* then led to heavier infection of seedlings, particularly when the seed was sown in sterilized soil.   It was therefore concluded that certain seed samples carry a bacterial surface flora capable of materially reducing infection by this pathogen under certain conditions (105, 146).   This work has been carried a stage further in the following experiments which included some under field conditions.   In the first place, it was shown by Petri-dish tests, in which seed were inoculated with a spore suspension of the· pathogen, that the surface flora of a sample of the variety Thatcher was more effective in reducing infection than was that of samples of the variety Reward, although evidence was produced which suggested that the difference lay in the greater number of organisms present instead of in their type.   Incubation of moistened seed prior to inoculation and sowing in sterilized soil produced similar results, although here the difference between the varieties was not pronounced.   In tests in unsterile soil seed were treated with one of the following: (*a*) suspension of bacteria from Marquis wheat incubated for 24 hours, (*b*) suspension of a bacterial culture increased on potato dextrose agar, (*c*) *a* and *b* together.   The seed

were also inoculated with the pathogen. After ten days disease ratings of eleven, nine and five were obtained for treatments (*a*), (*b*) and (*c*), respectively, compared with that of 31 for seeds not treated with these bacteria. Further evidence of the importance of the seed flora was provided by observations that seed from heads kept moist for three days before harvest gave seedlings showing far less disease in Petri-dish tests than untreated seed of the same crop. Further treatment of such " weathered " seed with formalin destroyed this effect (106).

It will be noted that the above experiments were carried out with seed artificially contaminated with spores and mycelium of *H. sativum,* and it is obviously pertinent to enquire whether similar control of disease would have been obtained with naturally infested seed or with seed carrying a deep-seated infection. Control under these conditions has in fact been obtained by using selected strains of *Chaetomium* spp. against *Helminthosporium victoriae* and *Fusarium nivale.* This work originated from the observation that certain Brazilian varieties of oats were not susceptible to the virulent pathogen *H. victoriae.* Resistance was shown both to the strains naturally occurring on these seeds and to the strains isolated from the susceptible variety Vicland. The resistance of the Brazilian varieties disappeared, however, when seed was disinfected by a hot water treatment. An investigation of the saprophytic flora of such seed led to the isolation of a number of strains of *Chaetomium cochlioides* and *C. globosum* which were antagonistic to the pathogen in pure culture. Certain of these isolates also controlled disease on Vicland oats when added together with the pathogen in sterilized or unsterile soil. It was therefore postulated that the resistance shown by the Brazilian varieties came from the antagonistic activity of the surface flora and in particular of certain species of *Chaetomium* (172). In an extension of this work, oat-seed naturally infected with *F. nivale* was used. Forty-eight isolates of various species of *Chaetomium* were tested in pot experiments for their ability to control disease when added as oat-straw cultures to unsterile soil. While the majority of the isolates were quite ineffective, some gave partial control and one gave almost complete control of disease. In field experiments good control of disease was obtained when a weight of an oat-straw culture of a suitable isolate of *C. cochlioides* equal

to the weight of seed was added to the drills at the time of sowing. Another isolate of the same species gave little or no control under these conditions. A large measure of control was also obtained by dipping infected seed in a washed suspension of ascospores and perithecia of the above isolate and air drying, or by soaking infected seed in a cell-free filtrate of a 96-hour shake culture of the antagonist for three hours before sowing. In terms of emergence and seedling injury the control was of the same order as that obtained by the use of a standard organo-mercurial seed dust. It is interesting to note that the isolate giving this result was not strikingly antagonistic to the pathogen in pure culture.

The antagonist, introduced as an oat-straw culture, persisted in air dried unsterile soil for at least six months. When infected seed was sown in such soil adjusted to a suitable moisture content, the control of disease, while less than at the beginning of the storage period, was still substantial. In this and other experiments the antagonist was frequently observed as perithecia on seed coats and on the surface of the roots of oat seedlings. The notable features of this work are therefore that very significant control of disease was obtained using naturally infected seed grown in unsterile soil under normal field conditions, that only one strain of one species of many tested was effective and that the antagonist apparently became established and persisted for some time in the soil into which it was introduced (173).

As further examples of the influence of microbiological factors on disease developing from seed-borne pathogens, the following may be quoted: the observations that plants from flax seed naturally or artificially contaminated with *Polyspora lini* or artificially infested with *Colletotrichum linicola* consistently showed more disease in sterilized than in unsterile soil (75); the control of disease caused by *C. linicola* in sterilized soil by various soil organisms (101); the reduction of damage to maize seedlings caused by *Penicillium oxalicum* when artificially contaminated seed were sown in very wet soil or inoculated with other species of *Penicillium* (41); the peculiar effect obtained by growing at high temperatures plants from maize seed infected with species of *Gibberella* when the seed-borne pathogen, now relatively inactive, caused a reduction in the damage caused by *Trichoderma viride*,

not normally considered pathogenic (48) ; the protection of wheat seedlings from attack by a species of *Helminthosporium* and of flax seedlings from attack by *Fusarium lini* by treating seedlings or the soil in which they were growing with a broth culture of an antagonistic bacterium (138).

MISCELLANEOUS DISEASES CAUSED BY SOIL-BORNE PATHOGENS. A number of diseases upon which a more limited amount of work has been done compared with those dealt with above will now be considered. They are all caused by soil-borne pathogens, and with one or two exceptions the methods of approach have been those already described. The Panama wilt disease of bananas caused by *Fusarium oxysporum cubense* has received some attention, possibly because it is very difficult to control by more orthodox methods and because the host is particularly difficult to work with genetically. A survey of Jamaican soils for the prevalence of actinomycetes antagonistic to this pathogen on soil solution agar showed they were unevenly distributed. From 66 samples 122 were isolated which showed antagonism in pure culture; of these, 66 were slightly active, 39 active and 17 very active. A somewhat unexpected result was that antagonism was frequently more pronounced on solutions of soil from which the organism was isolated. Field experiments with naturally infested soil tested the ability of five of the above very antagonistic organisms and four actinomycetes isolated from infested soil to control disease when added to the soil at planting time. Although no striking results were obtained, there was some evidence that these treatments either produced a small but significant increase in growth of the plant or a decrease in the number of diseased plants (119, 120). In a study of the rhizosphere flora of susceptible and resistant varieties of banana it was noted that a bacterium, strongly antagonistic to the pathogen, was isolated in high numbers from an immune variety but was virtually absent from the very susceptible Gros Michel variety (71).

In similar work with root-rot (*Fusarium culmorum* and *F. dianthi*) and wilt (*Phytomomas caryophylli*) of carnation, mass cultures of ten soil fungi selected for their antagonism to these pathogens were added to soil in a green-house bench, and a month later the pathogens were also added. After nine months growth two isolates of *A. scabies* had significantly reduced the amount of

infection by *F. culmorum* and *P. caryophylli*. *Aspergillus niger* was also particularly effective against the bacterium, but no control of *F. dianthi* was obtained with this or the other organisms. Where some control was obtained the active organisms could be isolated from the treated soil (167).

It has been noted that *Fusarium udum*, the organism causing wilt of the pigeon-pea, may be relatively sensitive to the activity of the soil micro-flora, since considerably more disease developed in sterilized than in natural soil when these were artificially infested with the pathogen (175). A related organism, *Fusarium lini*, causing flax wilt, has, however, been shown to be much less affected by biotic factors in the soil. Thus it persists in the soil for many years and rapidly accumulates under continuous cropping with the host plant. Of 88 isolates of bacteria, actinomycetes and fungi, 12 were antagonistic to this pathogen, but none strikingly so, and no control of disease was obtained in field plots when large quantities of cultures of *Bacillus subtilis, T. lignorum* or *Penicillium* sp., all antagonistic in pure culture, were added to the rows in which the seeds were sown. These antagonists were also ineffective against *F. lini* in steamed soil. Under the same conditions, consistently better control of disease of barley caused by *H. sativum* was obtained (8). In contrast with these results, when cultures of a species of *Chaetomium* were added to steamed soil infested with *F. lini*, a third of the plants survived at flowering, while plants in the control series were killed one week after emergence (166).

Turning now to rather different groups of fungi, one may mention the antagonism of a number of bacteria isolated from dead or dying leaflets of clover to the clover rot fungus, *Sclerotinia trifoliorum*, and the parasitism of sclerotia by species of *Fusarium* and *Mucor* (137); also the series of investigations with the sclerotium-forming basidiomycetes, *Hypochnus centrifugus, H. sasakii* and with the imperfect fungus *Sclerotium oryzae-sativae*, all soil organisms which may persist as sclerotia in soils for long periods. Some control of diseases of rice caused by these pathogens was obtained by adding to sand, organisms known to be antagonistic in pure culture or by inoculating sclerotia with these organisms before placing them on the leaf sheath of the host plant. In each case competition from organisms other than those deliber-

ately introduced was absent (50). Later reports mention active parasitism of sclerotia and mycelium of two of these fungi by *T. viride* (76, 77).

Another disease of rice, leaf blast, caused by *Piricularia oryzae,* has been reduced by immersing roots of seedlings in 0.05–0.1% suspensions of powdered mycelium of *Cephalothecum* spp. in water. These treatments improved seedling growth and reduced the numbers of leaf spots by about 50 per cent (190).

In concluding this section, reference will be made once again to the activity of the fungus *T. viride* in two somewhat different connections. Firstly, a series of papers have referred to the importance of this organism as a natural antagonist of the tree parasites *Fomes (Polyporus) annosus, Armillaria mellea* and *Polyporus schweinitzii* (12, 141–143). It has been shown to be of significance in preventing colonization of tree stumps by *F. annosus,* increased severity of this disease on alkaline soils being attributed to the absence of the antagonist under these conditions (143). More directly, it has been demonstrated that the pathogen failed to grow on acid humus (pH 4.2) underneath spruce trees but developed satisfactorily on this medium after it had been sterilized. No growth occurred, however, if at the same time *Trichoderma* sp. was introduced (170). In an entirely different connection this antagonist has been shown to be active against *Armillaria mellea* (19) which is a destructive parasite of the roots of a large number of plants. The work to be reported deals with the interaction of fumigation treatments and activity of the antagonist in eliminating the pathogen from soils of citrus groves in California. A variety of chemical treatments were effective, carbon disulphide particularly so. Field observations showed in the first place that the pathogen, established on roots or trunks of a suitable host and protected by a pseudosclerotial layer, is able to persist in the soil for many years and obviously therefore resists attack by soil organisms, including *T. viride.* It was also noted that this fungus was almost always associated with roots in which the pathogen had become non-viable as a result of fumigation. At first it was considered that this was due to the resistance of *T. viride* to the fumigant; it would therefore be the first fungus to colonize the mycelium of the pathogen after it had been killed by the chemical treatment. Further experiments under controlled conditions

clearly indicated, however, a more active role for this antagonist. The pathogen did not grow in pure culture in its presence nor could it be isolated from mixed cultures of both. *T. viride,* when added to infested soil, killed the fungus with no additional treatment; the fumigant, carbon disulphide, was, however, ineffective against the pathogen in the same infested soil in the absence of the antagonist, even when applied at rates normally effective under field conditions. The conclusions drawn from these experiments were that, while in natural soil *T. viride* does not become sufficiently dominant to destroy *A. mellea,* once the equilibrium of the soil microflora has been upset by treatment with fumigants, this antagonist rapidly dominates the partially sterilized soil and in this condition is able to colonize structures of the pathogen previously unaffected (20).

DISEASES CAUSED BY RUSTS AND POWDERY MILDEWS. As might be expected from their nature, there are relatively few records of the influence of saprophytes on the occurrence and development of these diseases. A number of workers have, however, studied the active parasitism of rust fungi by other organisms and have considered its significance in the natural control of certain diseases (1, 78, 92, 107, 118, 129, 162, 163, 171). There is little doubt that these hyperparasites are not uncommon. Thus an early reference records that *Darluca filum* had been found in association with 24 per cent of the rust species then recorded (1906) for Australia (118) and, more recently, that a bacterium attacking the fructifications of *Puccinia graminis* was obtained from many field specimens of plants infected with this pathogen (107). *Tuberculina maxima* has often been found parasitizing the fructifications of *Cronartium ribicola* in nature and is probably the organism which has been most extensively studied in relation to disease control. The bark cankers caused by the rust may be actively colonized by this fungus; this prevents formation of aecedia and pycnidia the following year. Some control of disease by introducing the saprophyte under natural conditions has been claimed in Germany, but similar attempts in the Pacific North-West of the U.S.A. failed, although it was noted that the parasite was established naturally in small areas (78, 163, 171).

The bacterium already referred to (107) was found to actively parasitize the fructifications of a number of other rusts under

green-house conditions and also inhibited the development of diseases on both adult plants and seedlings. A species of *Trichoderma* which did not prevent infection, did, however, curtail subsequent development of disease. A similar result has been reported for a species of *Alternaria* which colonized lesions on the leaves of *Rhus villosa* caused by *Hemileia vastatrix,* and, acting as a weak parasite, produced barriers of dead tissue which could not be penetrated by the rust (29).

Use of hyperparasites in the control of powdery mildew diseases would seem a little more promising, since the mycelium of these pathogens is almost entirely superficial in most species. *Cincinnobolus cesatii* is well known as a parasite of members of this group (49, 188), but its use in disease control does not seem to have been considered. An infusion obtained by incubating a suspension of manure in water and used as a spray has, however, been applied with some success in localizing infection caused by the powdery mildews *Sphaerotheca mors-uvae, S. humuli* and *Erysiphe polygoni.* A suspension of mycolytic bacteria isolated from rotting hay was also partially effective (40).

No results of practical importance emerge from the above; further work is likely to be confined to the part played by other organisms in the natural fluctuation of disease caused by these pathogens.

SMUT DISEASES. Here, in isolated cases, rather more significant results have been obtained. A number of bacteria have been shown to influence markedly the growth of smut fungi in culture and to retard the progress of infection (13, 82).

In one series of experiments, significant reduction of disease of maize plants was obtained when certain bacteria were added to the inoculum of the pathogen. Pre-inoculation of the plant with the bacteria, while still reducing the infection rating, was less effective under these conditions. Cell-free filtrates from cultures of the bacteria were ineffective. The bacteria used were originally isolated either from lesions which failed to produce galls after inoculation or as contaminants of plate cultures of the pathogen. One such isolate rapidly disintegrated detached smut galls placed in Petri dishes and behaved similarly with large galls which had formed in infected plants. In both cases chlamydospore formation was prevented. The activity of these or similar bacteria was

thought to account for the failure of some inoculations and for the disappearance of galls which is occasionally observed in the field (13). These results have been confirmed in work in which other organisms as well as bacteria were used. A species of *Trichoderma* and various bacteria inhibited chlamydospore germination; other bacteria caused considerable reduction. Three methods of inoculation were used in tests with living plants: in field trials by injecting a sporidial suspension into the base of the stem of maize seedlings or dropping a sporidial suspension into the leaf spiral, in pot trials by adding a sporidial suspension to the seeds before sowing. In each case the sporidia were added with and without one of the following antagonists, a species of *Trichoderma,* an actinomycete and two bacteria. While the addition of each caused some reduction of infection, only the *Trichoderma* sp. produced a substantial effect. It is interesting to note that this organism was partially effective when used in conjunction with a chlamydospore suspension on seeds sown in unsterilized soil (189).

Although not strictly relevant to the problem of disease control, the interaction between *Tilletia foetida* and *Tilletia caries* in the infection of wheat plants provides another example of the effect of one fungus on the growth of another. While plants infected with these pathogens commonly occur in the same field, the pathogens are rarely found on the same plant. This interaction was demonstrated experimentally by sowing seed free of or artificially contaminated with *T. foetida* in a field naturally contaminated with *T. caries.* The presence of *T. foetida* on the seed markedly depressed the development of disease caused by *T. caries* (14).

The further significance of the above work on the control and natural occurrence of these pathogens can not at present be properly assessed. As with the rusts, however, the possibilities of practical control seem rather remote.

STORAGE DISEASES OF FRUIT AND VEGETABLES. Organisms causing these diseases commonly enter through wounds. Once established, the primary pathogen may grow rapidly through the host tissue. The initial infection may be followed by a series of secondary infections, the rotted tissue finally containing a variety of organisms. In such circumstances it is not always easy to determine which organism, or group of organisms, is primarily responsible for the final damage, and it is therefore not surprising

that a number of investigations have dealt with the ways in which invasion of fruit and vegetable tissue by one organism may be influenced by others.   In one such series of investigations a number of pathogens responsible for rots of fruit or vegetables were studied.   In general terms the following types of association were found; predominance of one organism excluding others, free admixture of two or more organisms, the primary parasite followed by secondary saprophytes.   Temperature was found to play an important part in the development or suppression of organisms in mixed culture as was also the order in which the organisms were introduced into healthy tissue (114).   Similar results were obtained with citrus fruit, complex interactions following the introduction of more than one pathogen into susceptible tissue.   An increased rot was obtained with certain combinations, with others a reduction.   Again, temperature played an important part in deciding which organism of mixed inocula became dominant (53, 154, 155).   Further work along these lines has been reported for a species of *Penicillium* and *Diaporthe citri, Phytophthora parasitica* and *P. citrophthora* on citrus fruit (9, 61, 62), and for various organisms parasitizing apples (174).

WOOD-ROTS.   Investigations of the development of certain diseases primarily affecting the secondary xylem of trees under natural conditions have demonstrated the activity of saprophytes in preventing or impeding infection.   For example, *Phytophthora cactorum,* causing a crown rot of apple trees on artificial inoculation, is isolated readily only from the margin of lesions occurring naturally.   Evidence was adduced that the growth of the pathogen was inhibited by the growth of bacteria in all but the marginal regions (182).   Similarly, *Stereum purpureum,* which readily infects the surface of newly wounded woody tissues, does so much less readily a month later and is rarely able to establish itself on three-month-old lesions.   This was attributed to the colonization of the exposed surface by a variety of micro-organisms which then formed a barrier against invasion by the pathogen (25).   Similar effects have been reported for a bacterium against *Ophiostoma ulmi* on elm (73), a species of *Fusarium* against *Deuterophoma tracheiphila* on citrus (156), *Pseudomonas juglandis* against *Dothiorella gregaris* on walnut trees (52) and, at certain times of the year, between *S. purpureum* and *Nectria cinnabarina* or be-

tween the latter and *Botrytis cinerea* on plum trees (128). Studies with the black-knot disease of plums and cherry trees caused by *Dibotryon morbosum* have shown clearly how saprophytes may influence the development of this pathogen. It was observed that *Trichothecium roseum* appeared consistently each year during July and August on conidia-bearing stroma associated with knots on various *Prunus* spp. The fungus was sometimes restricted in its growth but at other times completely covered the fruiting surface. Inoculation of knots with a suspension in water of spores of the antagonist was followed three months later by the disappearance of perithecia and of the perithecial initials which were present at the time of treatment; uninoculated knots showed the normal number of perithecia. Under natural conditions it was noted that perithecia were always more abundant on non-infested than on infested knots and that there was a marked decrease in the number of new knots following heavy infection of old knots by the antagonist. From this and similar evidence it was concluded that *T. roseum* was of some importance in the biological control of *D. morbosum*. Ways in which such control could be enhanced were not reported (98).

LEAF DISEASES. Those caused by facultative parasites or saprophytes will be considered in this section. Comparatively little work has been reported. The rot of *Eichhornia crassipes* caused by *Hypochnus sasakii* was substantially controlled when leaves were simultaneously inoculated with *T. lignorum,* an active parasite of the pathogen in pure culture (117). This antagonist was also found to control the rot of lettuce leaves caused by *Botrytis cinerea;* a species of *Phoma* was also effective. Both antagonists gave better control when added as a suspension in malt or lettuce extract (10). More extensive work along these lines showed that a wide variety of organisms is able to control this disease when added to an inoculum of *B. cinerea* applied as a film over lesions simulating frost damage. Control was particularly effective at higher temperatures and enhanced by pre-inoculation of the saprophytes. Relatively few organisms were effective, however, at the lower temperatures which could be expected in the field and at which progress of the disease was still quite rapid. It was also shown that the pathogen was unable to penetrate areas of leaf tissue already colonized by certain saprophytes. Under conditions

which approximated to those prevailing naturally, a certain amount of control was obtained by spraying seedlings with a suspension of selected antagonists in a one per cent glucose solution (186). In associated work, a considerable amount of evidence was accumulated to support the hypothesis that the activity of saprophytes on dead or moribund leaf tissue substantially reduced disease of seedlings in seedbeds which were over-wintered in the open. Inoculation of seedlings during the winter with organisms isolated from moribund lettuce leaves failed, however, to control the disease. Some control of disease was nevertheless obtained by certain cultural methods which encouraged rapid colonization of dead tissue at ground level by saprophytes normally occurring in the soil (130, 131).

DISCUSSION AND GENERAL CONCLUSIONS

At this stage it will be convenient to deal separately with diseases affecting aerial parts of plants and those which damage roots or other organs below ground. In considering diseases of the shoot system, two general types of infection may be distinguished. In the first the pathogen enters through the intact surface of the host or through one of the natural openings such as stomata or lenticels; in the second entrance is through damaged or moribund tissue. The microbiological problems involved when antagonists are used to control these two types of diseases are likely to be quite different. The early stages of growth of a pathogen on the intact surface of a host are made in a film of moisture containing various substances which have diffused through the cuticle from the tissue beneath. The nature and amounts of such substances have been little investigated; both are likely to vary considerably between plant species and at different times in the life of the individual plant. It seems likely, however, that in its early growth on the host surface, the pathogen relies mainly on reserves within the spore. The antagonist, if it is to act upon the pathogen in the pre-penetration stage, would be subject to the same limiting nutrient conditions, and these would not normally be considered good for antibiotic production. On the other hand, this might be partially offset by the fact that fungi are generally more susceptible to toxins under poor nutrient conditions. Even if an antagonist were able to affect the growth of a pathogen in these circumstances,

it would also be necessary to ensure contact between the two unless antibiotics were produced of sufficient potency or in sufficient quantity to act at a considerable distance. In either case it would be necessary to cover the whole of the plant surface liable to infection, with spores of the antagonist, the density depending upon the efficiency with which the organism would act under these rather unsuitable conditions. Even assuming this could be done, another major difficulty would have to be overcome. Environmental conditions for germination and growth of the pathogen and antagonist would be very similar (a wider range for the antagonist would be desirable) so that one might anticipate that growth of the pathogen would be accompanied by growth of the antagonist over the whole area to which it had been applied. Any beneficial effect produced would therefore be non-persistent unless there were a periodic deposition of spores of the antagonist from elsewhere or unless the antagonist produced in the earliest stages of its growth, relatively resistant structures which remained *in situ*. With these considerations in mind one would naturally think of the spore-forming bacteria as a group of organisms most likely to act in these circumstances. The above remarks deal with the problem somewhat theoretically—at this stage this is inevitable in view of the lack of data on the nutrient conditions at the leaf surface and the nature and size of its natural microflora. In practice, at least on a small scale, it would not be difficult to alter both. The spores of many antagonists could easily be produced on a large scale and could readily be applied as a suspension in a nutrient medium. Some control of disease could then be predicted with some confidence and has in fact been obtained in isolated cases. Again, however, one would be faced with the non-persistence of the treatment unless conditions permitted multiplication of the antagonist after its germination and growth. Such conditions are less likely to be obtained in the open than under glass where some control of the environment at the plant surface would be possible. Once the antagonist were established in such a closed environment, it is not difficult to imagine the building-up of a population of antagonists which would have some effect on the growth and establishment of a pathogen. These and other considerations, which will not be dealt with here, would lead to the conclusion that theoretically this type of pathogen could be

controlled, even on a reasonable scale, by spraying plants with a suspension of suitable antagonists in a nutrient medium. Whether such control is likely to be worthwhile except in very special circumstances is very much open to doubt. Its only advantages would be in avoiding toxic sprays and in the rather remote possibility that it might become self-perpetuating. Otherwise it would seem as easy and much cheaper to apply an ordinary fungicide. Here at least one is assured of a certain level of persistence and avoids many of the uncertainties inherent in any biological method of control.

The second group of pathogens do not normally or can not penetrate the intact plant surface, and here considerations apply which are rather different from those outlined above. This type of pathogen normally enters through wounds or dying tissue which, it may be assumed, sooner or later become colonized by a saprophytic flora which does not normally spread to undamaged tissue. The pathogen must either get established before the saprophytes or be able to grow in their presence before spreading to healthy tissue. Evidence has been presented which shows that under natural conditions the microflora on damaged tissue may exclude a particular pathogen; it therefore follows that it might be possible to isolate the organisms responsible and introduce them or others obtained from similar habitats to the surface of the wound. At the same time it would be desirable to alter the nutrient conditions in directions favorable to the antagonist. As before, the problem of non-persistence might arise. Here, however, it might not be so acute, for it might well happen that moribund tissue would normally be produced continuously, thus providing new areas for the antagonist to colonize. This might happen, for example, if the pathogen normally entered through the dead or dying lower leaves of a plant which were closest to the soil surface, since the soil is probably the reservoir of most antagonists. It seems probable that in view of the greater availability of nutrients, antagonistic effects are more likely on the surface of wounded tissue than on intact surfaces of plants. On the other hand, if the normal microflora of the wounded surface is ineffective, greater difficulty might be experienced in introducing a more effective but different flora. Again, it is difficult to see what advantages a biological method of control would have over direct application of fungicides unless

colonization of the dead or dying tissue by an antagonistic flora could be obtained by a simple cultural operation, e.g., building up the soil around the bases of plants. With this, as with the other group of pathogens, direct application of selected antagonists is not likely to become a practical measure as long as alternative methods are available.

In considering diseases affecting underground parts of plants, two other factors assume importance. In the first place many of these diseases are very difficult or expensive to control by direct use of fungicides, and very often alternative methods are not available. There is, therefore, some justification for seeking somewhat unorthodox methods for controlling such diseases. Against this, however, is the fact that the pathogens causing such diseases act in the presence of a diverse microflora which is normally stable and resistant to change. Any radical and persistent alteration in this flora is, therefore, not easily obtained.

It will be convenient to deal first with soil-borne pathogens; these are not easily eradicated, once established, primarily because it is difficult to treat the large bulk of soil containing them. This is so even if the area of soil is not uniformly infested because it would not generally be easy to determine accurately the infested areas beforehand. It is apparent, however, that the spread and persistence of soil-borne pathogens may be very much influenced by soil conditions; soil invaders may be more susceptible than soil inhabitants in this respect. For both, the general problem is the same—how to modify the microflora in directions unfavorable to the pathogen. The method of approach to this problem has been largely empirical; this is inevitable, owing to our ignorance of the soil microflora and the lack of techniques for studying it in situ. Relatively little is known of the ways in which the behavior of the pathogen at the root surface differs from its behavior in the soil away from the roots, or of the effect of root exudates in modifying the saprophytic soil flora. There is, of course, good evidence that the composition of the rhizosphere flora is affected by both the type and condition of the plant. Most investigations of soil flora have used dilution plate methods. The types of organisms isolated in this way may well not be those preponderating in the soil as active mycelia. The heavily sporing species are more readily

isolated in this way, and it is these which have been used in most attempts to modify the flora by direct introduction of selected species. These attempts have been largely unsuccessful in the past and are likely to be so in the future unless conditions within the soil are altered at the same time. It is to be noted here that, since pathogens become established, there should be no reason why a particular antagonist should not behave similarly once the right conditions are found. Unfortunately these are not easily determined and the problem of establishing selected saprophytes in unsterile soil on a large scale is likely to be approached empirically for some time. As it happens, soil treatments favoring the growth of an introduced saprophyte may encourage the multiplication of similar types already present. This probably accounts for the fact that, so far, as good control of disease has been obtained by altering soil conditions as by adding antagonists.

There are few detailed studies in microbiological terms of the soil conditions in which pathogens disappear or become inactive. This is likely to be one of the more profitable lines of approach, particularly as it is now well known that the soil flora contains so many organisms antagonistic to particular pathogens in pure culture. In the past, unfortunately, pure culture studies have perhaps over-emphasized antagonism by the production of antibiotics. In spite of much work, the part played by antibiotics in the soil has still to be determined (21, 22, 51, 64, 65, 80, 81, 116). There is, however, some circumstantial evidence that it is significant. Many other factors may be at work, e.g., competition for essential metabolites, local pH changes, stimulation of growth in the rhizosphere. It may be significant that the Mucorales, probably one of the most important groups of soil organisms, are not well known as producers of antibiotics, even in pure culture; other features of their growth may account for their predominance. All these and other facts stress the importance of further detailed studies of the interrelationships between members of the soil flora and of the special relations between them and pathogens. Our knowledge at this level is still fragmentary, even for well known and important diseases, but in view of the tendency to increase the intensity of production and to grow the same crop continuously with the inevitable accumulation of soil-borne pathogens, it becomes

even more necessary to understand the ways in which use can be made of the natural antagonism between soil saprophytes and pathogens.

The problem of controlling soil-borne pathogens is considerably simplified in sterilized or partially sterilized soil. These treatments eliminate the pathogen which may, however, reinfest the soil later. It is generally much easier to establish selected antagonists in soil which has been treated in this way; the aim here would be to colonize the sterilized soil with a flora more antagonistic than the natural one and so prevent reinfestation. Any effect which is produced is likely to be temporary.

Turning finally to diseases caused by seed-borne pathogens, these would seem to be most amenable to control by microbiological methods primarily because the pathogen is confined to a small and known area of plant tissue. While it is unlikely that deep-seated infections will be controlled by applying antagonists externally, there is reasonable hope of success with more superficial infections or surface contaminations where it would not be a difficult matter to apply relatively large populations of antagonists either to the seed or to the soil in which the seed is sown. Various methods of application suggest themselves, such as adding the antagonist as a dust or a suspension to seed drills or to the seed itself, or using a slurry of the antagonist and an inert sticker or a readily available food material. These and similar methods are perfectly feasible and have been used with some success on a small scale (173). Inoculation of the seed with antagonists may not in fact be necessary as the surface is likely to carry a varied microflora which may be stimulated to activity by treatment with various nutrients and incubation under suitable moisture and temperature conditions. While these methods are novel and not impractical, it is not easy to see their advantages over more orthodox treatments such as application of fungicides to the seed or to the drills at the time of sowing. Indeed, while this type of disease is probably the easiest to control by biological methods, it is equally one of the easiest and cheapest to control with fungicides.

In conclusion it may be stated that no great success has attended the direct use of antagonists in control of disease up to the present, and, as far as can be seen, these methods of control are not likely to be able to compete with ordinary fungicidal treatments except

in isolated cases under special conditions. There is, however, a distinct probability that further investigation of the ways in which saprophytes influence the natural establishment and persistence of pathogens will lead to the development of cultural methods for controlling certain diseases, particularly if these are difficult or expensive to control in other ways.

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THE BOTANICAL REVIEW

THE VEGETATION OF ALBERTA

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INTRODUCTION

SCOPE OF REVIEW

The Province of Alberta, Canada, holds more than ordinary interest for botanists, especially for specialists in phytogeography, taxonomy and ecology. This is mainly because it is a region of vegetational transition zones. Here, two great plant formations, steppe and forest, come together, having east-west and north-south ecotones, as well as outliers, one within the other. Here also, is the meeting ground of east (Atlantic) and west (Pacific) floras or, more precisely, of boreal and Cordilleran elements. Moreover, in the north of the Province, transition from boreal to arctic begins.

Vast areas of the region are still unknown botanically, and many of the published reports are to be regarded as preliminary and tentative. Nevertheless, the literature is now of sufficient coverage and extent to warrant a review and general appraisal. Moreover, a synthesis of present knowledge would seem to serve a useful purpose in focussing attention on some of the main issues and unsolved problems. Not all aspects of our subject can be covered, of course, even within the compass of a fairly long review. Nor is it

necessary in this review to deal with certain topics, notably, problems of boreal-arctic vegetation and floristics. These and related topics have already been discussed in excellent articles by Raup (1941, 1946, 1947b). Certain other features of our plant life are arbitrarily excluded from consideration in this review, viz., algae, fungi, introduced plants and cultivated crops of all kinds. Publications dealing with taxonomic revisions of plants of our region also receive no attention, though references are made to available manuals, catalogues and species lists. The main emphasis is on synecological aspects of our vegetation, with particular reference to the prairie and forest associations of southern and central Alberta, the northern portion of the Province having been dealt with in recent comprehensive papers. The presentation is generally in terms of communities, succession and monoclimax; however, for certain mountain forests, the " continuum " concept and the climax as a " variable pattern " find favor. It is hoped that the review may interest those who are concerned with these concepts. Our discussion of prairie parkland includes a few excerpts from writings of early explorers. These and various later publications serve to show how our present understanding of the vegetation has been reached.

DESCRIPTION OF THE REGION

Only a general account of the physical features, soils and climate will be presented. Reference may be made to publications by Allan, Wyatt et al., Odynsky et al., Raup, Lewis et al., as well as to earlier papers by the present writer, for more detailed information.

PHYSICAL FEATURES. According to Allan (1943), Alberta has an area of approximately 255,285 square miles, and extends from the 49th parallel to lat. 60° north, a distance of 756 miles. The width of the Province averages about 325 miles. The west boundary is the Continental Divide in the Rocky Mountains north to about lat. 54°; it then follows longitude 120° to lat. 60°.

In Alberta there are four major physical divisions, namely, mountains, foothills, plains, and, lastly, the Precambrian area which is in the extreme northeastern corner of the Province and has an area of about 8000 square miles (Allan, 1943). The plains division comprises 87 per cent of the total area of the region. The lowest part of Alberta is in the northeastern corner, where the

altitude is about 650 feet above sea level. The plains division, often described as an undulating plateau, varies in elevation from 800 to 1000 in the north to about 3,500 feet along the eastern edge of the foothills belt. There are several prominences rising a few hundreds of feet above the surrounding plain, the highest including the Caribou Mountains in the north, the Swan Hills south of Lesser Slave Lake, and the Cypress Hills in southeastern Alberta. Sharp relief is provided by several great river valleys which run east and north. Lakes are very numerous in certain regions. In the south these are for the most part shallow basins (" sloughs ") which become partially dried up during the hot summer season. Northward the forested region is dotted with lakes, varying in size from a few hundred feet across to great bodies of water like Lesser Slave Lake, 50 miles long, and Lake Athabasca, 160 miles long. Many of the smaller lakes in the north are surrounded by peat bog. There is no sharp line of demarcation between the plains and the foothills belt. The foothills exhibit a rolling topography with elevations ranging generally from 3,000 to 5,000 feet above sea level. The mountain division (the Rocky Mountains) has elevations ranging from 3,500 feet along some of the valleys up to about 12,000 feet in the highest mountains.

GEOLOGY AND SOILS. The exposed strata in Alberta include rocks varying in age from the Precambrian to the early Tertiary age. In the mountains the oldest rocks are exposed, made up chiefly of limestones, sandstones, quartzites and shales. The soils within the mountains have been formed locally from these rocks (Allan, 1943). A recent report (Crossley, 1951) on the soils at Kananaskis, west of Calgary, appears to be the first detailed forest soil survey done in the Canadian Rocky Mountains and is an important contribution to knowledge of mountain soils and their relationships. A considerable proportion of the soils in the area of the survey are podsolic (brown and grey). In the foothills, Allan describes the rocks as folded and broken, consisting chiefly of sandstones, shales and coal seams. Most of the soils in the valleys and lowlands between the foothill ridges have been derived from the decayed rock on the ridges, and partly from outwash from the mountains. The plains are underlain, in large part, by rock formations chiefly younger and softer than those in the foothills belt.

Much of Alberta is covered by glacial deposits of Pleistocene age. Ice sheets from two sources extended over a large part of the plains and foothills of Alberta. The Keewatin ice sheet reached our region from the northeast and left debris chiefly from Pre-cambrian rocks. Cordilleran glaciers flowed eastward as a pied-mont ice sheet from the front of the mountains. This ice sheet left debris consisting largely of rock from the mountains where lime-stones and dolomites predominate (Allan, 1943). Large areas of Alberta are covered by resorted glacial deposits, and other large areas by alluvial and lacustrine materials transported by running water. Still other areas are occupied by residual material de-veloped from the underlying rock formations.

From these various deposits, through the action of climatic and biotic factors, the soils of the region have developed. Major soil zones, named after prevailing color of surface horizons are Brown, Dark Brown, Black, Transition (Grey Black) and Grey Wooded (Fig. 1). Following Wyatt et al. (1938–43) and Odynsky (1945a), these soil zones may be characterized briefly as follows. Brown soils, found in the semi-arid southeastern area, have a brown profile with an A-horizon of about five inches and a lime layer some 15 inches below the surface. Dark-brown soils have an A-horizon of about seven inches and a lime layer 20 to 24 inches below the surface. Black soils, found in the parkland region, where rainfall is higher and evaporation lower, have a black or deep brown horizon of 10 to 14 inches and a lime accumulation at 24–40 inches. Transition (grey-black) soils occur mainly in wood-land and show mixed profiles ranging from black to nearly grey. Grey-wooded soils characterize forested areas in much of northern and northwestern Alberta, and are relatively less fertile than the other types. They have developed under humid soil moisture conditions and have a surface horizon of semi-decomposed leaf mold, a severely leached and platy, greyish A-horizon of six to eight inches. Some of these grey-wooded soils are described as podsolic. Brief reference has already been made to soils of the Rocky Mountain region. Extensive peat areas also occur in central and northern Alberta.

CLIMATE. In general the climate of Alberta is representative of continental regions of northern latitudes, being characterized by a relatively low annual precipitation and by great extremes in tem-

perature between summer and winter seasons. However, striking differences in climatic conditions are found within the region. Southeastern Alberta has an average annual precipitation of about 12 inches, a high rate of evaporation, frequent hot dry winds and prolonged periods of drought. Northward and northwestward, the annual precipitation increases to about 18 inches in central Alberta and then decreases to 12 inches or less in northern areas. Over the same territory the evaporation rate decreases and hot winds are less frequent or rare. " In the more northern parts of Alberta the somewhat shorter growing season, the lower temperature, and the greater proportion of cloudiness compensate for the lower precipitation and make tree growth possible on most kinds of terrain " (Moss, 1952). Westward across southern Alberta the precipitation increases markedly to 20 or 25 inches in the foothills and to as much as 30 inches in the mountains. Sanderson (1948) classifies the foothills and mountains of Alberta as " moist subhumid ", having little or no water deficiency in any season. All other portions of the Province are said by Sanderson to have little or no water surplus in any season and are classified as " dry subhumid " to " semiarid ", the latter being the condition in the southeast.

FLORA—CATALOGUES, LISTS, MANUALS

The botanical classic " Flora Boreali-Americana " by W. J. Hooker (1829–40), based on collections of early explorers, contains the first comprehensive account of the plants of northern Alberta. Macoun's (1883–90) " Catalogue of Canadian Plants " includes records of his own extensive collections as well as earlier reports of species for Alberta as a whole. A few lists of limited scope were published in the early part of the present century, including that of Edith Farr (1907) on our mountain flora and one by Standley (1912) on the Mount Robson region.

Rydberg's (1917) Rocky Mountain Flora was the first manual assaying to cover Alberta, at least south of 55° N., and still is the only manual with that coverage of the Province. Rydberg's (1932) Plains Flora is quite useful for southeastern Alberta. A recent and very acceptable publication by Budd (1952), with descriptions of some 1200 vascular plants, covers the prairie and main parkland areas of the Province. Though a comprehensive manual for the

Alberta flora is still to appear, much of the necessary ground work has been done. Several lists and catalogues based on extensive field work have been published for representative areas. There has also been a certain amount of critical taxonomic work on some of the collections. First and foremost are the excellent annotated catalogues of Raup (1934, 1935, 1936, 1942) for portions of northern Alberta. Turner (1949) has provided a splendid list of the vascular plants of the south-central region, centering on Edmonton. For the Cypress Hills, in southeastern Alberta, Breitung's (1954) catalogue is an important contribution. Forthcoming catalogues covering some of our mountain areas are awaited with interest. Breitung has in manuscript an annotated list of the vascular plants of Waterton Lakes Park, and A. E. Porsild is preparing an illustrated manual on the Flora of the Rocky Mountain National Parks. Several of the ecological papers reviewed below contain lists of species and floristic notes. Reference should also be made to publications on the plants of areas adjoining Alberta. Of special significance are the critical studies of Porsild and Raup (1943) and Raup (1947a) on regions north of Alberta. The excellent Saskatchewan List by Fraser and Russell (1954) is consulted regularly by Alberta botanists, as also are the Flora of southern British Columbia (Henry, 1915) and the recent Supplement to this Flora (Eastham, 1947). A manual by Standley (1921) on the flora of Glacier National Park is quite useful for southwestern Alberta. Of interest, too, is the publication of a flora of Montana, the first part of which has appeared (Booth, 1950).

Reference may also be made to a number of semi-popular treatments of our flora and to certain briefer lists of species. Attractively illustrated books include the Alpine Flora by Brown and Schäffer (1907), the book on mountain wild flowers by Henshaw (1915), and the interesting account of wild flowers by McCalla (1920). A more recent book (Hardy and Hardy, 1949) on plants of the Rockies illustrates 200 wild flowers in color. A bulletin by Shoemaker (1938) on trees and shrubs in Alberta deals with native as well as exotic forms, especially in relation to their culture. Cormack (1948) lists the orchids of the Cypress Hills, with special mention of a few rare forms of *Orchis and Corallorhiza*. Groh (1949) has published notes on numerous native species, as well

as weeds, for Peace River and Fort Vermilion areas. Grasses of our region are described by Clarke et al. (1944), with particular reference to their identification by means of vegetative characters.

Though this review concerns itself mainly with vascular plants, special mention is made of bryophytes and lichens in connection with reports on certain types of vegetation. Species of these groups are listed in several of the papers reviewed. Reference may also be made to papers on lichens of the north by Lucy C. Raup (1928, 1930) and lichens of the mountain forest by Brinkman (1937); also to a list of Alberta liverworts by Brinkman (1923). Other papers on lichens and bryophytes by Brinkman are cited by Moss and McCalla (1946).

PHYTOGEOGRAPHIC PROBLEMS
(Relict Areas and Postglacial Forests)

Discussion of phytogeographic topics is largely excluded from the present review. However, a brief presentation of certain of these topics is required as a setting for a consideration of synecological data. Apart from the subject of phytogeographic regions or life zones (see below), there are intriguing floristic problems that demand at least passing mention.

As has often been pointed out, Alberta is a meeting ground of eastern and western floras. This is exemplified by pairs of closely related species (vicariants), such as *Pinus banksiana* and *P. contorta, Abies balsamea* and *A. lasiocarpa, Populus balsamifera* and *P. trichocarpa,* in eastern and western regions. These floras present interesting problems concerning the origin and history of our vegetation, especially in terms of Pleistocene events and more recent climatic fluctuations. Various outliers of Boreal and Cordilleran vegetation, one within the other, serve to complicate the picture. However, critical study of the outliers as possible relict areas of a former vegetation, may actually help to clarify our understanding of the past. Alberta provides a somewhat similar situation in its Steppe-Forest transition (discussed later in this review).

Possible Cordilleran relict areas are the tops of the Caribou Mountains, the Swan Hills and the Cypress Hills. There is some evidence that these areas escaped glaciation as nunataks, but whether any vegetation survived on these nunataks is problem-

atical. In a recent discussion of the Cypress Hills, Breitung (1954) says it is not improbable that the submontane forest and grassland actually persisted there during the last glaciation. He notes, however, that Russell (1951) favors the view that the Cordilleran biota reached the Cypress Hills in early post-glacial time, subsequent to the northeasterly retreat of the ice front. As the climate became warmer the Cordilleran element withdrew to the higher elevation of the Hills, to become segregated from the mountains by a broad belt of prairie.

Unglaciated areas in our foothills region may have served as refugia for biota during the period of the Wisconsin ice-sheets. Though the Cordilleran and Keewatin sheets coalesced at several points during times of greatest advance, it is unlikely that they united along the entire front. The pertinent geological evidence has been reviewed by Hansen (1949a, 1949b, 1950, 1952) in connection with his pollen analyses of peat sections in Alberta and British Columbia. Hansen (1950) reaches the general conclusions that " an ice-free corridor, 100 miles or more in width, existed between the Keewatin and Cordilleran ice sheet during the late Wisconsin glaciation " and that " the abundance of spruce and pine . . . as indicated in the lowest horizons of peat bogs in the region, suggests that this ice-free area was forested during Late Wisconsin or soon thereafter ". Forests of this foothills refugium are believed to have been centers from which biota migrated into progressively deglaciated areas. Alternate advances and recessions of the ice-sheets flanking the refugium may have occurred, bringing about corresponding shifts in the vegetation and possibly isolation of biota (as relicts) in certain locations.

Of further interest in this connection is the refugium believed to have existed during the Late Wisconsin in the upper Yukon River valley. " How extensive an ice-covered area separated the unglaciated portion of Yukon Territory and the ice-free corridor of western Alberta during the Late Wisconsin glacier is at present conjectural ". Whether pine and spruce, migrating northward from western Alberta or southward from the Yukon, were the first to reach the intervening region, is impossible to say (Hansen, 1950). Involved here is Hultén's (1937) theory of the persistence of plants in unglaciated refugia in the Yukon and Alaska, and especially his view that continental western American radiants

from a Beringia center had migrated southward before the Wisconsin glaciation and persisted in ice-free areas close to or within the icefront during at least the Late Wisconsin stage (Hansen, 1949b). With particular reference to peat profiles of bogs in west-central Alberta, Hansen suggests that they may record pre-Late-Wisconsin forests that had persisted in an ice-free corridor during this glacial stage, and so lend support to Hultén's view.

A review of Hultén's (1937) important contribution to phytogeography is beyond the purview of the present article, but the following references are to be noted. In the light of Hultén's theory, Halliday and Brown (1943) draw certain inferences with regard to the relationship of some forest tree species to present climate and the possible course followed in their repopulation of the Canadian land-mass following Wisconsin glaciation. Hultén's work has been discussed in comprehensive articles by Raup (1941, 1946, 1947a, 1947b). Of special significance would appear to be Raup's critical examination of the flora of the Mackenzie Mountains in the light of Hultén's thesis concerning the origin and dispersal of all arctic and boreal floras.

PHYTOGEOGRAPHIC REGIONS (Life Zones)

Several attempts have been made to define biogeographic areas, such as life zones, biotic provinces, vegetation belts and phytogeographic regions. The general result is one of considerable confusion in concepts and terminology. For our present purpose, a modified form of Halliday's (1937) classification has been adopted (Fig. 1 and Table I). To justify our concepts and terms, also to show the bearing on pertinent synecological categories, the following review is presented.

Merriam's well known life zones, though now largely discredited, are worthy of some attention here. Odum (1953) points out that a " major life zone ", as understood by European ecologists, is not the same as " life zone " as used in North America. On this Continent " life zone " generally has reference to a series of temperature zones proposed by C. H. Merriam in 1894 and widely used by zoologists. According to Odum, the original temperature criteria have been abandoned, and Merriam's life zones are currently based on the distribution of organisms. Indeed, these zones have tended to become community zones, actu-
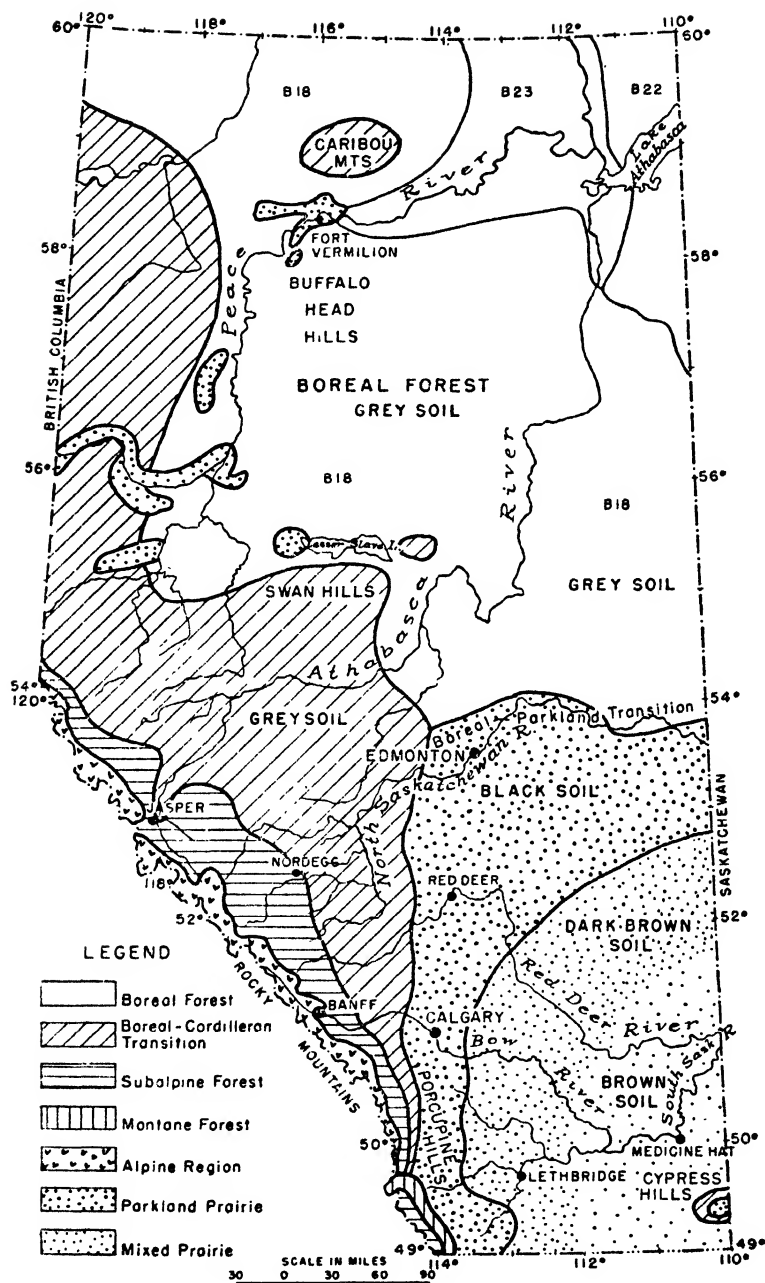
Fig. 1. Outline map of the Province of Alberta, showing the main phytogeographic regions.

TABLE 1

Phytogeographic regions	Sections (According to Halliday)	Chief communities
Prairie (Steppe) Mixed Prairie (Brown Soil Belt) Main Parkland Prairie (Black Soil Belt) Peace River Parkland		Stipa-Bouteloua (Spear grass—Grama grass) Festuca scabrella (Rough fescue) Agropyron-Stipa (Wheat grass—Spear grass)
Boreal-Grassland Transition	Aspen Grove (B17)	Populus tremuloides (Aspen) Marsh and Reed Swamp
Boreal Forest (Northern Coniferous)	Mixedwood (B18) Northern Coniferous (B22) Mackenzie Lowlands (B23)	Picea glauca (White Spruce) Picea mariana } Bog Forest Larix laricina Pinus banksiana (Jack Pine) Populus (Aspen) (Balsam Poplar) Pinus contorta var. latifolia (Lodgepole Pine)
Boreal-Cordilleran Transition	Foothills (B19)	
Cordilleran Forest Subalpine Forest Montane Forest	East Slope Rockies (SA1) Douglas Fir and Lodgepole Pine (M5)	Picea engelmanni-Abies lasiocarpa (Spruce-Fir) Pseudotsuga (Douglas Fir) Pinus flexilis (Limber Pine)
Alpine		Miscellaneous Communities

ally biome divisions or subdivisions in all but name. Most of
Alberta is included in Merriam's Boreal Region, only the south-
western plains area falling in the Arid Transition Zone of his
Austral Region. The Boreal Region is subdivided by Merriam
(1898) into three zones: Arctic-alpine, represented in Alebrta by
the treeless alpine areas of the Rocky Mountains; Hudsonian,
which includes the northern forested part of our region and also a
similar belt just below the timberline southward along the
mountains; Canadian, which includes the forest lying between the
Hudsonian Zone and the Transition Zone, as well as a belt below
the Hudsonian in the mountains. During the early part of the
present century, various authors adopted this system, though often
with major changes in boundaries and in application of terms.

Daubenmire (1938, 1946) shows how different efforts to de-
limit Hudsonian and Canadian zones in the Rocky Mountains have
proven inadequate and often inconsistent. While recognizing
Merriam's life-zone work as the first major attempt to use climatic
data in interpreting the distribution of North American biota,
Daubenmire concludes that life zones based on temperature are
untenable and are best delimited as major climax plant associations.
Moreover, he maintains that Merriam's terms are arbitrary and
meaningless; therefore, they should be abandoned in favor of more
descriptive names that apply to precise concepts, e.g., Engelmann
spruce–subalpine fir zone. Use of the terms " Hudsonian " and
" Canadian " for subdivisions of the Transcontinental Region or
Northern Coniferous Forest has proven no less fortunate. Dice
(1943), for example, recognizes as Hudsonian a " biotic province "
that includes the entire Northern Coniferous Forest east of the
Rocky Mountains, and as Canadian a " biotic province " com-
prising the hardwood forest climax of the Great Lakes and east-
ward. According to Dice, approximately the northern half of
Alberta is Hudsonian, while the Cordilleran and Plains portions
of our region fall, respectively, in his Montanian and Saskatchewan
biotic provinces. Broad divisions similar to the " biotic provinces "
proposed by Dice are by no means new. For northern and western
Canada, Dice's Eskimonian, Hudsonian, Montanian and Saskatche-
wan correspond closely to the Arctic, Transcontinental (Boreal),
Western (Cordilleran) and Prairie (Plains) Regions of various
authors, e.g., Adams and Senn (1945). The latter terms appear

to have the advantage of being fairly descriptive and generally understood.

Significant as these major biotic regions may be, more ecological interest probably attaches to their major subdivisions, especially those commonly recognized as biotic associations. Reference may be made here to the terms " montane " and " subalpine " for subdivisions of the Western (Cordilleran) Region. These have been variously employed by different authors, including Rydberg (1917), Halliday (1937) and Spilsbury and Tisdale (1944). According to Daubenmire's (1946) critical analysis, the Subalpine Zone is approximately the Hudsonian Zone as usually understood; it is also the *Picea-Abies* association of Weaver and Clements (1938) and the spruce-fir zone of Daubenmire (1942). The Montane Zone is included in the Canadian Zone of earlier authors and is the *Pinus-Pseudotsuga* association of Weaver and Clements; it is equivalent to the Douglas-fir zone of Daubenmire. Actually, the term " montane " has been variously applied, as have " Hudsonian " and " Canadian " already discussed. Daubenmire (1946) wishes to reject the term " subalpine " for any one unit because subalpine vegetation differs considerably from one mountain system to another. He suggests that the only terminology free from these criticisms is that based upon the dominant and characteristic species of a zone, e.g., " Engelmann spruce-subalpine fir " zone.

In the light of foregoing considerations, a vegetational classification is presented (Table I) which incorporates features of Halliday's (1937) forest system and which aims to relate familiar concepts and terminology of biogeographers, foresters and ecologists. Halliday's classification has the advantage of utilizing terms that are, in the main, descriptive of the vegetation types or of the terrain. His designations (B17 to M5) for different forest subdivisions are included in Table I for the benefit of Canadian foresters and others who use the system. Of the concepts and terms proposed, " Montane " is perhaps the least satisfactory for our purpose. As will be explained later, the so-called Montane Forest, as it occurs in Alberta, is recognized rather better by shrub and herb strata than by the characteristic tree dominants. Despite Daubenmire's objections to " Subalpine ", this term is retained as being generally understood and readily applied in our region. We

prefer to treat Halliday's Foothills Section (B19) as a Boreal-Cordilleran Transition rather than a Section of the Boreal. Any one particularly interested in the forests of northeastern Alberta should be aware of Raup's (1946) criticisms of Halliday's Sections B22 and B23. The main purpose of Table I is to set forth the relationship of the various phytogeographic regions and sub-divisions to the chief plant communities of Alberta, as these have been defined by recent investigators.

Delimitation of still smaller biotic areas is proposed by Strickland (1938) in a paper on the Diptera of Alberta. He recognizes and maps 21 " ecological areas " on the basis of original vegetation, present utilization (ranching, wheat-growing, irrigation), soil, elevation and precipitation. A few of these areas relate definitely to present land-use and therefore they appear somewhat unrealistic in terms of natural biota; but, nearly all conform quite well to current ecological views.

PRAIRIE (Steppe) VEGETATION

MIXED PRAIRIE (*Stipa-Bouteloua* Association)

This grassland characterizes the brown soil zone and much of the dark-brown soil zone of southeastern Alberta. Clarke (1930), in his pioneer grazing-land studies, refers to the vegetation of the brown soil zone as a short-grass formation comprising two chief types which he designates *Bouteloua-Stipa-Koeleria* and *Agropyron-Poa* associations. Moss (1932) speaks of the same region as Southern Prairie and gives *Bouteloua gracilis, Stipa comata, Agropyron smithii* and *Koeleria gracilis* as the dominant species. The term " Short Grass " for the prairies of the brown soil zone was perpetuated by Clarke et al (1942) and others, while the grassland of the dark-brown soil zone was designated " Mixed Prairie ". It is generally agreed now that the " short grass " phases (dominated by *Bouteloua gracilis*) of the region are to be interpreted as edaphic climax or as disclimax. However, Hubbard (1950) is definitely of the opinion that a " Short Grass " formation should be recognized for much of the brown soil zone. From exclosure and soil texture studies, he concludes that prairie dominated by *Bouteloua gracilis* is not merely a disclimax caused by grazing. Coupland (1950), whose work is reviewed below, seems to have achieved a satisfactory classification.

Moss (1944) reports a "*Bouteloua-Stipa* Association" for the southwestern part of the dark-brown soil zone. On the assumption that *Stipa comata* is the climax species of the Mixed Prairie, Moss and Campbell (1947) refer to this grassland as the *Stipa comata* association. They draw a boundary line between this grassland and the *Festuca scabrella* association to the north and west. This line extends through the dark-brown soil zone and represents the ecotone between the two communities.

An extensive and thorough investigation of the Mixed Prairie in Canada has been carried out by Coupland (1950). Though most of Coupland's work was done in Saskatchewan, numerous studies were made in Alberta, and his main conclusions may be taken to apply to our region. According to Coupland, the Mixed Prairie or *Stipa-Bouteloua* association is dominated by six grass species, namely, *Stipa comata, S. spartea* var. *curtiseta, Bouteloua gracilis, Agropyron dasystachyum, A. smithii* and *Koeleria cristata,* while a seventh grass, *Muhlenbergia cuspidata,* is a dominant in eroded areas. Twelve other grass species and four sedges are also characteristic, though not ranking as dominants. The chief sedge is *Carex eleocharis.* Composites and legumes are the most abundantly represented families of dicotyledons. Leading forbs include *Artemisia frigida, Phlox hoodii, Malvastrum coccineum, Pulsatilla ludoviciana, Gutierrezia diversifolia, Sideranthus spinulosus, Chrysopsis villosa, Artemisia gnaphalodes,* and species of *Solidago* and *Potentilla.* Important shrubs are *Rosa arkansana* and *Artemisia cana.*

From analyses of data obtained by the point-transect method of sampling, Coupland recognizes six well-defined types in the mixed prairie. Five of these, ranked as faciations, are regarded as fully developed (climax) types, and the sixth (the *Agropyron-Muhlenbergia* facies) is subclimax as a result of erosion. The *Stipa-Bouteloua* faciation is the most extensive. It is the prevailing type on medium-textured soils upon glacial till deposits in the moister part of the brown soil zone and the drier part of the dark-brown soil zone. Approximately 60 per cent of the total vegetation of this grassland type is said to consist of three grasses, *Stipa comata, S. spartea* var. *curtiseta* and *Bouteloua gracilis,* though these occupy only 12.8 per cent of the soil surface. The vegetation is composed of three layers, the upper consisting of the culms of mid-

grasses and the flowering stalks of taller forbs, the middle layer characterized by *B. gracilis, Carex eleocharis* and certain shorter forbs, the lowermost being a mat of *Selaginella densa.* The *Bouteloua-Stipa* faciation occurs on areas of medium- to coarse-textured soil in the drier part of the brown soil zone, on areas of coarse-textured soil in the moister part of this zone and in exposed situations throughout the region. The *Stipa-Agropyron* faciation characterizes areas of higher moisture efficiency. The *Agropyron-Koeleria* faciation occurs on soils developed on uniform clay deposits occupying the beds of former glacial lakes. A variant of the latter faciation, with *Agropyron smithii* as the sole dominant, occurs on slightly alkaline clay flats and on certain alluviated clay flats. The *Bouteloua-Agropyron* faciation occupies clay loam, solonetzic soils particularly eroded patches ("burn-outs"), in the drier part of the brown soil zone in southwestern Saskatchewan. The cactus, *Opuntia polyacantha,* is widespread in this type, ranking next in abundance to *Artemisia frigida.* Whether the *Bouteloua-Agropyron* faciation is prevalent in Alberta appears somewhat uncertain. Coupland says that the solonetzic soils of southeastern Alberta are coarse-textured and support the *Bouteloua-Stipa* faciation. Solonetz soils in Alberta have been mapped and described by Odynsky (1945b), but the native vegetation associated with these soils awaits adequate study, especially in the northwestern part of the brown soil zone and extending northward through the dark-brown and black soil zones.

In the various climax faciations recognized by Coupland, grasses and sedges compose 84 to 95 per cent of the total basal area, the forbs and shrubs 5 to 16 per cent of the basal cover. A considerable portion of the entire mixed prairie has been modified by overgrazing. Vegetational changes caused by grazing have been adequately discussed by Clarke (1930), Clarke and Tisdale (1936), and Clarke et al. (1942). In general, overgrazing is said to have resulted in decreased vigor of the mid-grasses and of plants furnishing palatable browse. In dry locations a consocies of *Bouteloua gracilis* is the common indicator of overgrazing. Under severe grazing and trampling, *Carex eleocharis* gains in density at the expense of the grasses. For further information on the ecology of the mixed prairie in Canada, including significant observations on many of the leading species, Coupland's excellent monograph should be consulted.

MAIN PARKLAND PRAIRIE (*Festuca scabrella* Association)

This is the characteristic prairie of the black soil zone and aspen grove belt of southwestern and central Alberta.   It extends eastward into Saskatchewan as a belt north of the Mixed Prairie.   It is also the grassland of the parkland area on the plateau of the Cypress Hills in southeastern Alberta.   The dominant species, *Festuca scabrella,* is properly described as a bunch grass; yet, in our region it appears generally to form short rhizomes that serve to enlarge the tussock.   In the last edition of Hitchcock's (1950) Manual, this species is described as "rarely producing a slender rhizome".   It may be noted here that some authorities treat *F. scabrella* as a sub-species or variety of *F. altaica* Trin.

HISTORICAL CONSIDERATIONS.   Recognition of this grassland as a distinct and important type has come only recently, though the region covered is extensive and the dominant grass forms conspicuous tufts with long leaves and culms.   Our observations indicate, however, that this species forms very few flowering stalks in some years.   John Macoun (1882), usually a keen observer and accurate reporter, makes no mention of *Festuca scabrella* for our region; indeed, he seems to have confused this species with *Stipa spartea.*   The latter he refers to as "northern buffalo grass".   He says this is the famous grass of the hills in the Bow River country and forms the bulk of the winter pasture.   He states, too, that as hay it is equally as good as grass, for, having produced next to no seed, the whole of the nutriment is laid up in the leaves.   "It is not true of our Buffalo grass that the seed is among the leaves as it is in Kansas", writes Macoun.   Evidently he was referring, at least in part, to *Festuca scabrella,* though there was surely considerable *Stipa spartea* var. *curtiseta* in the same grassland, and it is strange that the awns of that grass did not impress him.   Failure to recognize the fescue (as such) may have been because of the paucity of culms formed by that grass in the seasons of Macoun's travels across the prairie.   It seems likely that other observers have failed, for the same reason, to note the dominant role of this species.   Macoun (1882) does recognize one of the chief tall dense grasses of the Cypress Hills plateau as a species of *Festuca.*   Clarke (1930) reports *Festuca scabrella* as one of the leading grasses of benchlands in southern Alberta.

In a brief account of the parkland prairie (called Northern

Prairie) of south central Alberta, Moss (1932) reports *Festuca scabrella* as one of the chief grasses, along with *Koeleria gracilis, Agropyron* spp. and *Avena hookeri*. The dominance of *F. scabrella* in the grasslands of southwestern Alberta, the Cypress Hills, and portions of the park belt was recognized by Clarke et al. (1942) in their " submontane " type of mixed prairie, termed the *Festuca-Danthonia* association. The chief grasses are said to be *Festuca scabrella* (dominant), *Koeleria gracilis, Agropyron subsecundum, Danthonia parryi, D. intermedia* and *Festuca idahoensis*. For the southwestern black soil region of Alberta, a *Festuca-Danthonia* association, described by Moss (1944), further emphasized the significance of *Festuca scabrella* in our vegetation. According to Moss, the dominant grasses are *F. scabrella, F. idahoensis, Danthonia intermedia* and *D. parryi*, of which the *Danthonia* species are localized in their dominance, and *D. parryi* is largely restricted to the western part of the region. Characteristic associated grasses include *Koeleria gracilis, Agropyron griffithsii, A. dasystachyum, A. trachycaulum, Stipa spartea* var. *curtiseta, S. columbiana, Poa cusickii* and *Avena hookeri*. Listed also as members of this association are some 12 grasses of secondary importance, six sedges, seven shrubs and over 65 forbs. The association is discussed in various of its relationships, including the transition to the *Bouteloua-Stipa* association eastward, correlations with climatic data and with soil zones, the prairie-woodland ecotone, and affinities with the so-called " Northern Prairie " of the aspen grove belt to the north and northeast. The latter problem is considered more fully by Moss and Campbell (1947) in their treatment of the *Festuca scabrella* association as the climax grassland for the entire aspen parkland (Fig. 1).

CLIMAX GRASSLAND. The *Festuca scabrella* association is envisaged by Moss and Campbell as the climax grassland and also the virgin prairie of the parkland belt. A sharp distinction is drawn between this association, in which *Festuca scabrella* is the sole dominant, and fescue grassland produced by mowing for hay or by moderate to heavy grazing. The latter grassland shows a marked reduction in the fescue and an increase in secondary species, notably, *Agropyron trachycaulum* (including *A. subsecundum*), *Stipa spartea* var. *curtiseta, Koeleria cristata* (*K. gracilis*) *Agropyron dasystachyum, Danthonia* spp., *Carex* spp.

and certain forbs.   Listed for the climax association are some 150 species of higher plants.   Of these, about 125 are described as " characteristic " and 70 as " constant " members of the association.   Many additional species are recorded for the modified fescue grassland.   Some 50 species found in the southern portion of the association are not recorded for the north, while only four species in the north are not noted for the south.   The richer flora of the southern part of the association is explained in terms of proximity to a variety of other vegetational types, especially of the mountains, and in terms of the time element, insufficient time having elapsed since glaciation for certain southern species to have reached the north.   Of the grasses found only in the southern part (south of the Red Deer River), *Festuca idahoensis* and *Danthonia parryi* call for special mention, for these are the chief species associated with *Festuca scabrella* in the *Festuca-Danthonia* association described by Moss (1944).   Inclusion of this association in the *Festuca scabrella* association by Moss and Campbell (1947) is based on the interpretation of *F. scabrella* as the climax dominant and the other two species as subclimax.   Of particular interest is the role of *Danthonia parryi*.   This grass is said to dominate in localized areas, especially on exposed, wind-swept slopes north of Waterton Lakes Park and in the Porcupine Hills, behaving as an edaphic subclimax species and as a disclimax under heavy utilization.   According to a recent report by Hanson (1953), this grass is very prominent in the present condition of our ranges, especially in the Porcupine Hills, producing more forage there than any other single species.   Hanson further reports that this species is replaced, in the mountain valleys to the west, by *Danthonia intermedia*, a smaller and less palatable species.

The *Festuca scabrella* association, as it occurs on the plateau of the Cypress Hills, has been described for the Saskatchewan portion of the Hills by Coupland and Brayshaw (1953) and by Breitung (1954) for both Saskatchewan and Alberta parts of the Hills. Coupland and Brayshaw report that the association occurs there on black soils, that there is an abundance of the shrub *Potentilla fruticosa*, and that the chief grasses are *Festuca scabrella* (dominant and occupying an average of 55 per cent of the nonshrubby cover in the sites sampled), *Agropyron subsecundum, Danthonia intermedia, Helictotrichon hookeri (Avena hookeri)*

and *Stipa spartea* var. *curtiseta,* while secondary grasses are *Koeleria cristata, Agropyron smithii, A. dasystachyum* and *Muhlenbergia richardsonis.* Breitung places the associated grasses in a somewhat different order of prevalence and gives a few others as being common, e.g., *Festuca idahoensis* and *Poa interior.* Common and conspicuous forbs include *Pulsatilla ludoviciana, Cerastium arvense, Achillea millefolium, Erigeron glabellus, Gaillardia aristata, Galium boreale, Lupinus argenteus* and *Hedysarum alpinum* var. *americanum.* Breitung says that two of the most striking features of this prairie are its color and luxuriance, the grassland in certain seasons becoming a veritable flower garden. Seventy years earlier Macoun (1882) wrote in similar vein as follows: " The grasses of the plateau are so tall that for miles at a time we had great difficulty in forcing our way through them . . ." and " In all my wanderings, I never saw any spot equal in beauty to the central plateau of the Cypress Hills ".

The fescue grassland of the aspen grove belt of western Saskatchewan, as described by Coupland and Brayshaw (1953), is similar to that already discussed for adjacent Alberta. The importance of *Festuca scabrella* varies from complete dominance in the northern fringe to co-dominance with *Stipa spartea* var. *curtiseta* in the northern part of the dark-brown soil zone. Throughout all of the black soil zone the fescue is much more abundant than *Stipa.* In Clementsian language, the fescue community is described as postclimax to the *Stipa-Agropyron* faciation of the mixed prairie, the latter commonly occuping exposed locations within the aspen grove region, such as south-facing slopes and tops of knolls; the fescue community is preclimax to aspen forest. The general appearance of this grassland is the same as in the Cypress Hills of Saskatchewan except for the absence of *Potentilla fruticosa.* Quantitative data are presented concerning the composition and structure of the grassland. On the basis of an analysis of these, it is concluded that the grassland of the Cypress Hills and the northern fringe of the aspen grove belt in Saskatchewan is part of the *Festuca scabrella* association as described by Moss and Campbell (1947). In these areas, which are characterized by the more moist black soils, *F. scabrella* occupies about 55 per cent of the basal cover provided by herbs. The principal subdominants are *Agropyron subsecundum, A. trachycaulum,*

Danthonia intermedia, Helictotrichon hookeri, Koeleria cristata, Muhlenbergia richardsonis, Stipa spartea var. *curtiseta* and *Carex* spp. The chief forbs are said to be *Cerastium arvense, Achillea millefolium, Galium boreale* and *Anemone patens.*

It is concluded by Coupland and Brayshaw that the *Festuca scabrella* community of Alberta and western Saskatchewan can not be considered to be allied to any of the six grassland associations previously described in North America (Weaver and Clements, 1938) and should therefore be considered as a seventh association of the grassland formation. The eastward extension of the *Festuca scabrella* association evidently requires further investigation. Coupland and Brayshaw say that they could not be certain that this type of vegetation is climax eastward of Saskatoon. Preliminary studies indicate that the ecotone between the fescue grassland and the true prairie to the southeast (Weaver and Fitzpatrick, 1934) is very wide and varied in composition.

The prairie vegetation of the park belt in Alberta and Saskatchewan is closely related to the grasslands of Idaho and other parts of the northwestern United States, and also to those of south-central British Columbia. This was pointed out by Clements and Clements (1939) in a brief discussion of " submontane " prairie. Important elements of the Palouse prairie of western Idaho and eastern Washington, notably, *Festuca idahoensis, Stipa columbiana, Agropyron spicatum, Lithospermum ruderale, Geranium viscosissimum* and *Balsamorhiza sagittata*, are said by Moss (1944) to extend into Alberta. Hanson (1953) emphasizes a floristic continuity from the Palouse prairie, through the valleys of British Columbia and mountain passes into Montana and southern Alberta, to the foothills of Alberta, supporting the theory that many of our species have moved in from the southwest along these routes. Of interest here is Tisdale's (1947) study of grasslands in the southern Interior of British Columbia. The three vegetational types recognized by Tisdale are linked by the chief dominant, *Agropyron spicatum,* into one major community. *Festuca scabrella* is reported as abundant and often co-dominant. In fact, the most mesic of the three grassland types is dominated by *A. spicatum* and *F. scabrella.* Tisdale states that the abundance of *F. scabrella* in southern British Columbia seems to link the grassland there with that of the foothills in Alberta.

PEACE RIVER PRAIRIE (*Agropyron-Stipa* Association)

This grassland is associated with poplar and willow groves to form parkland areas on dark soils in the generally forested Peace River region (Fig. 1). Earlier work on this vegetation by Raup (1934, 1935) and others is reviewed in a recent paper by Moss (1952). The grassland is described by Moss as an *Agropyron-Stipa-Carex* community, comprising three subtypes or faciations, viz., *Agropyron-Carex* on low areas, *Stipa* on dry slopes and *Agropyron-Stipa* on mesic sites. For the entire community 154 vascular species are recorded, and for the *Agropyron-Stipa* faciation, which is the most common prairie grassland of the region, 139 vascular species, consisting of 36 graminoids, 84 forbs and 19 woody species. This faciation is interpreted as the " climax " grassland of the region and accordingly might well be given the status of a plant association. On this interpretation the whole community may be designated the *Agropyron-Stipa* association. The chief grasses and sedges in the climax type are *Agropyron trachycaulum* (including *A. subsecundum*), *Stipa spartea* var. *curtiseta*, *Koeleria cristata*, *Stipa richardsoni*, *Carex obtusata* and *C. praticola*. Leading forbs are *Galium boreale*, *Achillea millefolium*, *Thalictrum venulosum*, *Geum triflorum* and *Solidago* spp. Common shrubs are *Symphoricarpos* spp., *Rosa* spp. and *Amelanchier alnifolia*. Characteristic species of the *Agropyron-Carex* faciation of low moist areas include *Agropyron trachycaulum*, *Carex atherodes*, *Schizachne purpurascens*, *Bromus* spp., *Calamagrostis* spp., *Hierochloe odorata*, *Carex praticola* and *Vicia americana*. The sharply contrasting *Stipa* faciation of xeric situations, such as river valley slopes, includes *Stipa spartea* var. *curtiseta*, *Stipa columbiana*, *Agropyron dasytachyum*, *Koeleria cristata*, *Artemisia frigida* and *Pulsatilla ludoviciana*. The presence of a cactus, *Opuntia fragilis*, on these dry slopes and at a latitude 56° is of some interest. Worthy of note is the absence of *Bouteloua gracilis* and *Stipa comata*, common grasses of similar habitats in south-central Alberta.

The *Agropyron-Carex* faciation has evidently succeeded a marsh community characterized by coarse grasses and sedges, including *Calamagrostis inexpansa* and *Carex atherodes*. These prominent members of this faciation are interpreted as relict species that have persisted from the lower community. Upon further drying of the

lowland areas the *Agropyron-Carex* faciation develops into the climax *Agropyron-Stipa* type. The *Stipa* faciation of xeric areas may be followed by the climax type as these areas become more mesic through gradual levelling of the terrain. Evidence is presented by Moss that the *Agropyron-Stipa* grassland is not the climatic climax vegetation of the region, but instead an edaphic climax. There is a marked tendency for willow and poplar to encroach upon the grassland areas; but succession to forest has long been effectively retarded by fires and by special physiographic and edaphic features of these areas, notably poorly drained and inadequately aerated soils.

The Peace River grassland as described by Moss (1952) is evidently closely related to the prairies described by Raup (1935) for Wood Buffalo Park in northeastern Alberta and northward. The relationship between these grasslands and those of the arctic tundra constitutes "one of the most intriguing problems of the north" (Raup, 1941). The Peace River grassland has rather close floristic affinities with the *Festuca scabrella* association. Its climax type is dominated by the leading secondary species in the fescue grassland, namely, *Agropyron trachycaulum, Koeleria cristata* and *Stipa spartea* var. *curtiseta;* but there is one outstanding difference, viz., the absence of *Festuca scabrella,* the dominant species of the fescue association. It seems, therefore, that the Peace River prairies can not be included in the *Festuca scabrella* association, which Coupland and Brayshaw (1953) have proposed as a seventh association in the grassland formation of North America. Nor can the Peace River prairies be classified as part of the Mixed Prairie association because of the absence of such grasses as *Bouteloua gracilis* and *Stipa comata.* It is suggested, therefore, that the *Agropyron-Stipa* association of the Peace River region might be considered as an eighth association in the grassland formation of North America.

PARKLAND (Grove Belt)

GRASSLAND-WOODLAND ECOTONE

Typical parkland may be described as a mosaic of prairie patches and aspen groves, with prairie occupying the drier situations and aspen the more moist and sheltered places. The main parkland extends as a fringe along the foothills of southern Alberta and

northeastward as a broad belt across the south-central part of the Province to the Saskatchewan border. Smaller isolated parkland areas occur in the Cypress Hills, the Hand Hills, and in the general Peace River region (Fig. 1). Transition from parkland, whether to open prairie or to forest, is usually gradual. The following account of our main parkland, written nearly a century ago, is quoted here as an important early report and as a description that applies even to-day to relatively undisturbed portions of our parkland: " In this district the woods are very scanty and consist almost exclusively of aspen poplar, which form small groves and artificial-looking clumps that dot the rich pasture lands " and "As the country towards the south merges into the open prairie, the clumps of copse and young poplars are found only nestling on northern exposures. The last outliers of the woods to the south generally consist of ' islands ', as they are called, which make a show from a distance, but when approached are found to consist of small species of willow " (Palliser, 1863).

The parkland, as a transition or tension belt, actually comprises thousands of true tension lines or ecotones, these occurring where aspen and prairie communities meet (Moss, 1932). Such ecotones consist of representatives of the two competing communities, including certain grasses and shrubs, notably *Symphoricarpos occidentalis*. In some situations the aspen invades the grassland by extending its roots and forming suckers that establish there as trees. This tendency for aspen to invade and replace prairie vegetation has been reported for different parts of the parkland (Moss, 1932, 1944, 1952). Counteracting this tendency are various agencies, such as burning, grazing, damage by rabbits, and desiccating winds. The extent to which poplars reproduce by seed and establish new stands in the parkland and prairie regions is problematical. At some time in the past, either in comparatively recent years or many centuries ago, the thousands of isolated aspen groves of the parkland must have been initiated by seed. Various aspects of this problem have been discussed by Moss (1932). The question of the transfer of viable seed and the establishment of seedlings was investigated by Moss (1938) for our region. Longevity of poplar seeds under natural conditions is from two to four weeks, and establishment of the seedlings occurs only when the surface layer of the soil is continuously moist during at least

the first week of their growth.   This is said to be due to the slow growth into the soil of the primary root and also to absorption being largely dependent upon a brush of delicate hairs near the soil surface.   It seems, therefore, that new poplar groves are likely to arise in our region under rather exceptional climatic conditions.

Explanations of the origin and persistence of prairies, especially where there is evidence of current or former woodland invasion, are of perennial interest.   Some of the early explorers evidently believed that our parkland prairies were originally well forested.   Palliser (1863) reports the region south of the Battle River and north of the Neutral Hills, near the Alberta-Saskatchewan border, as old forest land with good soil, the forest having been destroyed by fire and the region now dotted with small poplar clumps.   According to Palliser, that portion of fertile country lying between his " triangle " (the Canadian extension of the central American desert having for its base the 49th parallel from longitude 100° to 114° W., with its apex reaching to the 52nd parallel of latitude) and the present forest to the north was once heavily timbered.   It was thought to contain a large spruce element, for Palliser's Report reads: " Sometimes a small clump of the spruce fir has been left by the fire " and " From Fort Carlton to Edmonton, a distance of nearly 400 miles, there were not more than five or six spots where any of the coniferae were left ".   Dawson (1879) reports that there can be no doubt that the prairies of the Peace River have been produced and are maintained by fires.   It seems to have been assumed by many early writers, also by pioneer settlers, that the Indians set fires for the express purpose of maintaining the grassland.   These earlier ideas have tended to prevail, along with another popular belief that the buffalo (bison) had an important part in maintaining the prairies.   The " master hand of climate ", especially the precipitation-evaporation factor, has been increasingly emphasized by investigators (Borchert, 1950).   This writer makes the trenchant comment that " Grassland climates favor fire, just as they favor grass whether there are fires or not ".

Burning has doubtless been very effective in counteracting natural succession to woodland in the days of the Indians and buffalo as well as more recently.   Where settlers have operated to prevent fires, the woodland has often extended at the expense of the prairie.   For the parkland regions of Alberta, the importance

of the pyric factor has been emphasized by Moss (1932, 1952, 1953a), also by Moss and Campbell (1947). But these authors, like several other recent investigators of prairies, point to additional aspects of the problem. They agree with Borchert (1950) as to the "master hand" played by climate. Moreover, like Borchert and others, they realize the significance, not only of prevailing conditions but also of major climatic shifts of the past, as revealed by evidence from soil profiles, peat pollens and relict vegetation. For example, the degraded black soils presently found on the forested fringes of our main parkland are thought to have been formed under grassland. Thus various lines of evidence suggest the theory of a xerothermic period, a late post-glacial, pre-historic period, with more frequent and prolonged drought conditions than currently prevail in our grassland regions. This period is believed to have seen considerable extension of prairies. At the end of the xerothermic period and the return of somewhat cooler and more humid conditions, the adjacent forest began slowly to invade the grasslands, being more or less retarded, however, by the pyric and biotic factors already discussed. Indeed, prairie has tended to persist on hot dry situations, such as south-facing slopes, especially where these are swept by drying winds. Even today, prairie species occur as relicts on dry slopes in the northern forest, far beyond the main parkland regions. Other examples of physiographic and edaphic factors making for the persistence of prairies in localized areas have already been mentioned in this review. It should be noted in passing that more than one prolonged warm dry period may have occurred during postglacial time. Even in historical times a dry cycle, 400 to 1100 A.D., is said to have occurred (McComb and Loomis, 1944). During this period there may have been a temporary set-back to tree invasion and some return of woodland to prairie.

Of special interest here are the prairies of northwestern Alberta. The suggestion has been made (Moss, 1952) that the existing prairie patches of that region, especially the drier of these, might well be interpreted as remnants of a very extensive grassland which occupied much of the region during the xerothermic period and might even have been connected with the main parkland of south-central Alberta. The numerous floristic elements common to the Peace River and more southern prairies suggest a community of

origin for these grasslands.   This hypothesis finds support in the recent work of Hansen on pollen analysis of peat sections in Alberta.   Indeed, Hansen (1949) suggests that the Peace River grasslands may be relicts of a postglacial expansion of prairie " during a warm, dry maximum between 8,000 and 4,000 years ago ".   On the other hand, Raup (1934, 1935) sees no need to postulate a warm-dry segment of time for the boreal region and envisages only a gradual amelioration of the climate since glaciation.   He stresses the probability of a fairly short postglacial period for the introduction and establishment of vegetation in the region. During this period our northern grasslands may have developed from tundra through subarctic grass-sedge stages.   The strong *Carex* element in the Peace River grasslands may be significant in this connection.

These interrelated phytogeographical problems will doubtless be clarified through further study of peat profiles and of subarctic " prairies " (Moss, 1952).   Possibly our main parkland prairie followed the coniferous forest north in the xerothermic period, while the prairies of northern Alberta and adjacent regions developed, at least in part, from subarctic grasses and sedges.   The absence of *Festuca scabrella* from the northern prairies may be significant in this connection.   These considerations suggest to the reviewer still another aspect of the parkland-prairie enigma, viz., various effects of the availability of species for establishment in different areas.   For example, would the main Peace River grassland be characterized by *Festuca scabrella* had that species reached the region centuries ago?

GRASSLAND AND SOILS

Various aspects of grassland in relation to climate and soils have been mentioned earlier in this review.   Of some interest in connection with the development of grassland soils is a suggestion put forward by Moss and Campbell (1947).   They support the view generally held by students of climate-soil-vegetation relationships in steppe-woodland regions, that black or chernozem soils are essentially grassland soils developed through many centuries in a cool continental climate of moderate rainfall; that the steppe or prairie areas, likewise the black soil areas, were originally larger than now, and have been invaded by forest rather recently in soil

history; that the black soils thus covered by forest have been modified by podsolization to become degraded or transition (grey-black) soils. Emphasizing their conclusion that the natural vegetation of the black soil and grey-black soil zones of our main parkland was through many centuries a *Festuca scabrella* association, in which a single species predominated, and assuming that most of the organic matter in prairie soils has derived directly or indirectly from the roots and crowns of grasses, these authors conclude that the bulk of the organic substance in the black soils was produced by the dominant grass species, *Festuca scabrella*. Even in the dark-brown soil zone, this grass seems to have flourished to some extent and no doubt has furnished that soil with much organic material.

It is suggested, therefore, that a large proportion of the agricultural wealth represented by the black and related soils of Alberta had its origin in the activity of just one kind of higher plant. This claim may appear slightly exaggerated, especially when one considers the possibility of certain other grasses having dominated in earlier stages of the grassland's history, also the possibility of other grasses having been abundant under buffalo grazing, and moreover, when one thinks of various associated shrubs and forbs, especially the legumes, which may have been more prevalent in the virgin prairie than they are today. In any event it is worthy of note that the organic matter of our black soils has derived from quite a different primary source (in terms of main plant species) than that of either the dark soils of the Peace River prairies or the brown soil of southeastern Alberta.

FOREST VEGETATION

POPLAR (*Populus*) Association

Of the six species of poplar native to Alberta, four are confined to southern and southwestern regions, where they occur mainly in river and stream valleys. These will be considered later in this review. Two of the species, the aspen or white poplar (*Populus tremuloides*) and the balsam or black poplar (*P. balsamifera = P. tacamahacca*), are widespread in the Province, comprising extensive pure stands and also being associated with other tree species, on many kinds of terrain. The aspen occurs over a wide range of edaphic conditions, including dry knolls, moist river flats

and such soils as loam, clay and sandy. The balsam poplar is more restricted in its occurrence, reaching its best development in the more moist situations, such as river flats (Moss, 1932). While these species are found throughout the forest regions of Alberta, their greatest concentration is in the south-central part, adjacent to the main parkland (Halliday and Brown, 1943). Northward and westward, poplar tends to be replaced by conifers. As already indicated in this review, aspen is the characteristic tree of parkland areas. Moreover, it is regarded as the climax species of the main parkland of Alberta (Moss, 1932), as also of corresponding parts of Manitoba and Saskatchewan (Bird, 1930).

The entire poplar vegetation of central and northern Alberta is regarded as an association, within which aspen and balsam poplar consociations are recognized (Moss, 1932, 1953a). Poplar stands are usually even-aged; this is explained by the fact that the trees of a stand start as suckers after a complete burning off of the parent stand. The aspen rarely exceeds 120 years in age, the balsam poplar 135 years. For the poplar association in central Alberta somewhat over 200 plant species are cited, of which only about 50 vascular plants and a very few mosses are regarded as important constituents. For the community in northwestern Alberta, some-what similar records have been published and certain minor floristic differences noted.

Typically, the poplar association consists of five strata: (a) taller trees, forming a nearly continuous canopy; (b) smaller trees and larger shrubs, an intermittent layer, usually poorly developed in the aspen consociation; (c) lower shrub layer, rich or sparse, and more or less obscured in summer by the next stratum; (d) taller herbs, often an almost continuous stratum and quite prominent in the latter part of the growing season; (e) lower herbs, including mosses and lichens, forming a carpet which locally is continuous, especially in the balsam poplar consociation. Bands of mosses, especially *Pylaisia polyantha,* are common on tree trunk bases.

Characteristic species of the balsam poplar consociation include: the dominant tree, *P. balsamifera;* the shrubs, *Cornus stolonifera, Ribes* spp. and *Lonicera involucrata;* the herbs, *Mertensia paniculata, Equisetum* spp. and *Petasites palmatus;* and the mosses, *Hylocomium splendens* and *Aulacomnium palustre.* Characteristic

species of the aspen consociation include: the dominant tree, *P. tremuloides;* the shrubs, *Symphoricarpos albus, Amelanchier alnifolia* and *Shepherdia canadensis;* and the herbs, *Cornus canadensis* and *Maianthemum canadense.* Prominent in both consociations are: the shrubs and small trees, *Rosa woodsii, R. acicularis, Viburnum edule, Rubus idaeus* and *Salix* spp.; the herbs, *Rubus pubescens, Aster ciliolatus, Vicia americana, Lathyrus ochroleucus, Pyrola asarifolia, Fragaria glauca, Galium boreale, Epilobium angustifolium, Viola rugulosa, Thalictrum venulosum, Calamagrostis canadensis* and *Agropyron trachycaulum;* and the mosses, *Pylaisia polyantha* and *Mnium cuspidatum.* Certain leading species of the poplar association in central Alberta, notably *Corylus cornuta, Prunus* spp., *Aralia nudicaulis* and *Disporum trachycarpum,* are said to be much less common in northwestern Alberta. On the other hand, the poplar community of the latter region includes a few Cordilleran species not listed by Moss (1932) for central Alberta, e.g., *Salix scouleriana, Spiraea lucida, Arnica cordifolia, Arctostaphylos rubra* and *Castilleja raupii.* It may be noted here, however, that Turner (1947) has reported the first two of these species, as well as several other Cordilleran species, near Pigeon Lake, more than 100 miles east of the Rocky Mountains in south-central Alberta.

The poplar vegetation of the Rocky Mountain region of Alberta has received relatively little study. The aspen poplar consociation of the parkland and outer mountains in southwestern Alberta has been described briefly by Moss (1944). Aspen groves of this region are said to be generally of low stature for their age, growth in height having been retarded by the prevailing winds. Those in the more exposed positions have truncated tops and the characteristic wind-blown habit. This community is compared with the aspen consociation of central Alberta and found to be sufficiently alike in physiognomy, internal structure and floristic composition to be classified as a variant of the same aspen consociation. Minor floristic differences are noted, including the presence in the south of such Cordilleran species as *Rubus parviflorus* and *Spiraea lucida.*

The aspen poplar woods of the Cypress Hills have been described briefly by Breitung (1954). These woods occur chiefly on the northern slopes of the Hills and along the lower edge of the pine

forest. Groves on exposed sites are stunted and low in stature, with " branchy ", wind-blown crowns, caused by strong, desiccating winds. Available information indicates that this vegetation may be treated as a variant of the aspen consociation, being most closely related to the phase of this consociation in southwestern Alberta. Cordilleran species prominent in the aspen community of the Cypress Hills include *Salix scouleriana, Bromus marginatus* and *Elymus glaucus.*

<center>EFFECTS OF BURNING</center>

A poplar stand that has been burned off is usually soon replaced by a dense growth of young trees, with only a temporary alteration in the associated vegetation. Certain species, including *Epilobium angustifolium, Aster* spp. and some of the shrubs and grasses, become quite prominent; but, after two or three years, these are suppressed by the young poplars and there is a gradual return to the original composition of the community. Cutting of poplar stands produces essentially the same results (Moss, 1932).

Fireweed, *Epilobium angustifolium,* is a striking feature on burned forest areas in our region. A study of the ecology of this species by Moss (1936) revealed facts bearing upon its abundance on burned land, and led to the discovery of an interesting anatomical character, namely, rings of cork in the wood of the underground organs. The sudden appearance of fireweed, generally attributed to wide dissemination of an abundance of seed, is explained in terms of proliferation of shoots from old deep-seated roots and rhizomes. Interxylary cork may relate to the persistence of these organs. Incidentally this discovery of internal cork in fireweed led to the finding of rings of cork in the wood of certain other plants, notably a species of *Artemisia* (Moss, 1934). Later reports of this structure (Diettert, 1938; Moss, 1940; Moss and Gorham, 1953) include discussions of its adaptational aspects in sage-brushes (*Artemisia* spp.) and various other plants.

<center>SUCCESSION TO SPRUCE</center>

Natural succession of poplar to white spruce (*Picea glauca*) is clearly indicated throughout central and northern Alberta. Ecesis of spruce occurs in poplar stands of various ages, where seed is available, and under appropriate ground conditions. The young spruce grow slowly for many years; but as the poplar thins out

with advancing age the suppressed spruce come to overtop the poplar. This tendency of the spruce to supersede poplar is counteracted by biotic and pyric factors. Considerable damage is done to young spruce by snowshoe rabbits and other animals, but periodic burning is the major factor operating against succession to spruce. While a severe burn gives only a temporary setback to the sucker-regenerating poplar, it is devastating in its effects on spruce (Moss, 1953a). Poplar in relation to other forest vegetation will be discussed later in this review. Invasion of prairies by aspen poplar has been considered above.

BOREAL (NORTHERN) FOREST

WHITE SPRUCE (*Picea glauca*) Vegetation

The white spruce of Alberta is generally reported as *Picea glauca* var. *albertiana*. However, there is considerable evidence that typical *Picea glauca* occurs also and that it merges with the variety in some parts of the Province. Until further study has been given to this taxonomic problem, the designation *Picea glauca* seems preferable. White spruce is the leading species of the Boreal Forest and Boreal-Cordilleran Transition regions (Fig. 1), if not in actual coverage, at least as the potential dominant. To a limited extent, it extends into the Subalpine and Montane Forest regions, where it grows at the lower elevations. In these regions, and also in the higher foothills, it merges with Engelmann spruce (*Picea engelmanni*). Where these species grow together, intermediates (hybrids) between them are said to be quite common. White spruce also occurs in the Cypress Hills.

Picea glauca ASSOCIATION. This has been recognized as the chief type of white spruce vegetation in Alberta. For central Alberta this association is described briefly by Moss (1932). It is commonly found in habitats similar to those occupied by the balsam poplar consociation and has many species in common with that consociation. The associated trees and shrubs are rather few and sparsely scattered. They include *Populus balsamifera, Cornus stolonifera, Viburnum edule* and species of *Salix, Ribes* and *Rosa*. The herbaceous and moss flora is variable and generally patchy. Where the spruce forms a close canopy, there is usually a continuous ground cover of various mosses, chiefly *Hylocomium splendens, Hypnum schreberi* and *Ptilium crista-castrensis*. Where

the stand is more open, this characteristic " feather moss " stratum is not so well developed, and certain herbs are often abundant there; these include *Linnaea borealis* var. *americana, Equisetum* spp., *Calamagrostis canadensis, Cornus canadensis, Mitella nuda, Rubus pubescens* and *Pyrola* spp. White spruce is said to be the natural successor to balsam and aspen poplar and to behave as the climax species of the region.

The white spruce vegetation is said to extend into northwestern Alberta, where it has been described by Moss (1953a) and interpreted as the climax forest vegetation for mesic sites there. Of four variants (faciations) of the association described by Moss, two are said to be prevalent: (*a*) *shrub-herb faciation:* the spruce generally not crowded; usually a strong admixture of poplars and the willow, *Salix bebbiana;* a prominent shrub stratum with *Viburnum edule, Ribes* spp. and *Rosa* spp.; and luxuriant herb strata with *Linnaea borealis* var. *americana, Rubus pubescens, Mertensia paniculata, Fragaria* spp., *Pyrola* spp., *Epilobium angustifolium, Calamagrostis canadensis, Cornus canadensis, Mitella nuda, Viola renifolia* and *Petasites palmatus.* (*b*) *feather moss faciation:* the spruce forming a fairly close canopy; shrubs and herbs relatively few and sparse; an almost continuous carpet of *Hylocomium splendens, Calliergonella* (*Hypnum*) *schreberi* and other mosses, with associated horsetails (*Equisetum* spp.), bunchberry (*Cornus canadensis*) and other species. These and other faciations of the association intergrade to form various mixtures, depending upon the terrain, the age and density of the spruce, and the past history of the area, especially in terms of burning. The feather moss faciation is regarded as the association climax, for, in the absence of burning the other faciations tend to develop into this type, the spruce gradually supplanting the shorter-lived poplar and birch, while most of the shrubs and herbs are replaced by mosses. " On the other hand, it seems doubtful whether this community is self-perpetuating as such, either following burning or subsequent to old age and decadence of the spruce" (Moss, 1953a).

The white spruce forests of northeastern Alberta and adjacent Mackenzie region have been described by Raup (1933a, 1946). Three divisions of these forests are distinguished, namely, flood plain spruce, upland mesophytic spruce, and parklike white spruce.

The first two of these types appear to be similar to the white spruce association of northwestern and central Alberta, the flood plain type being somewhat like the shrub-herb faciation described above, and the upland mesophytic type resembling the feather moss faciation. The subject of retrogression of spruce to poplar and pine following various kinds of forest fires and subsequent return to spruce has been well described by Raup (1946) for northern regions.

The white spruce forests of the foothills and mountains of Alberta have been given relatively little study. Recent reports by Bloomberg (1950) and Horton (1954) will be discussed later in connection with Cordilleran forests. For the Carbondale River area, in the mountains of southwestern Alberta and falling within the Montane Forest region, Cormack (1949) describes the virgin s] ruce forest, in which white spruce is thought to be the dominant species. However, since alpine fir (*Abies lasiocarpa*) is reported as common in the virgin stands and since many other Cordilleran and Montane elements are indicated, this forest, too, will be discussed under a later heading.

A brief account of the white spruce forest in the Cypress Hills by Breitung (1954) indicates that this forest might well be classified as a variation of the *Picea glauca* association of Alberta. Though closely associated with lodgepole pine stands and despite a few Cordilleran elements, this forest seems to resemble more closely the white spruce association of central and northern Alberta than spruce forests of the mountain region.

PARKLIKE WHITE SPRUCE FOREST. As noted above, this is one of three divisions of the white spruce forests described by Raup for northeastern Alberta. There it occurs mainly on high sand ridges, stony beaches and dune habitats near Lake Athabasca. It consists of open parklike stands with little or no undergrowth but often with a ground cover of fruticose lichens and mat-forming shrubs. The drier phase of this forest, as it occurs on sand, is somewhat like the white spruce vegetation described by Moss (1932) for a sandhill area near Edmonton in south-central Alberta, though differing markedly in floristic composition. Raup (1946) discusses the bearing of habitat, climate and species history on some of the anomalies of parklike spruce and jackpine forests in northern regions.

SUCCESSIONAL RELATIONSHIPS.   White spruce is generally considered the climax species in vast areas of central and northern Alberta, as well as in parts of the foothills and lower mountain valleys.   Succession of pine and other coniferous vegetation to spruce will be considered later.   Here further attention is given to poplar-spruce relationships.   Many observers have reported ecesis of white spruce in poplar stands and succession to spruce. White (1915), for example, points out that aspen makes an excellent nursetree for the spruce and claims that if fires are controlled the poplar will gradually be replaced by spruce.   In a poplar stand, young spruce usually grow slowly for many years, apparently because of shading by the poplar.   But, as the poplar thins out with advancing age, the suppressed spruce grow rapidly and may eventually over-top the remaining poplar.   This situation is often met with in poplar stands of 70 years and older (Moss, 1932).   Thus the white spruce may succeed the poplar; and under the dense shade of the spruce the characteristic subsidiary species of the white spruce association gradually replace those of the poplar community.

The severity of a burn has a profound influence on the subsequent forest, due to the differences in the habit of reproduction of the poplar and spruce.   " Light fires, which merely burn over the top of the humus layer, stimulate suckering of aspen and encourage a vigorous growth of perennial minor species (shrubs and herbs) on the forest floor.   Spruce is dependent on small seed for its regeneration, therefore it finds the above conditions of severe competition unfavorable for establishment.   The result is generally the development of a pure poplar stand.   On the other hand intense fires, by consuming the entire humus layer, simultaneously reduce the vigor of the aspen suckers, eliminate most of the minor vegetation and expose mineral soil, making possible the rapid invasion of spruce,—provided always that seed is blown in and subsequent climatic conditions are favorable.   In the latter eventuality, a spruce stand with scattered poplar is likely to result ".   (Rowe, 1953).   Proximity of parent trees as a seed source has been generally recognized as crucial.   Spruce trees do not produce seed in quantity until they are at least 35 years old, and generally not until 45 to 60 years old.   Therefore recurring fires have the effect of eliminating the spruce and maintaining poplar forest.   As al-

ready stated, this actually is the situation in vast areas of central Alberta for which white spruce is the potential dominant.

However, setting aside the effects of periodic burning and assuming a spruce seed source, there still remains some doubt about the extent of spruce reproduction in poplar stands. This problem of spruce regeneration is now receiving critical study. Rowe (1953), in a discussion which emphasizes the complexity of forest site and the importance of giving due recognition to site as an " ecosystem ", makes an interesting comment on the conditions affecting establishment of spruce in poplar stands. He draws attention to the mechanical action of accumulating litter on plants of the forest floor, and reports that " field observations have shown that much of the mortality of the initially small spruce seedlings under hardwood and mixedwood stands can be attributed directly to smothering by poplar leaves ". Another aspect of white spruce reproduction, that of mechanical disturbance of the forest floor, is being studied in forests of the Rocky Mountains by Crossley (1952).

The fate of the so-called white spruce climax, in the form of old decadent stands that remain unburned, is also problematical. In general, it seems that young spruce do not root at all well in the moss stratum and deep duff of old spruce stands but that there is often considerable reproduction on decaying logs and stumps. This problem will be discussed further in connection with our review of Cordilleran forests.

BOG FORESTS AND BOGS

The pioneer work on peat bogs in Alberta by Lewis and Dowding (1926) deals with the structure, vegetation, peat and history of small bogs (muskegs) in the vicinity of Edmonton and points to several problems presented by these bogs. Formed on fine glacial clay in small basins in morainic areas, these bogs are characterized by *Sphagnum* moss, with black spruce (*Picea mariana*) as the dominant tree and Labrador tea (*Ledum groenlandicum*) the leading shrub. However, *Sphagnum* is tending to disappear and to be replaced by vegetation indicative of drier conditions. Desiccation is caused at least partly by fires. Retrogression due to inflow of springs highly charged with mineral matter to form calcareous lakes in a peat basin is also reported.

Further studies reported by Lewis et al. (1928) deal with Sphagnum and birch bogs, bog forests, low-moors (cariceta) and reed-swamps of central Alberta, in various of their inter-relationships. The main results of these studies will be discussed below in relation to more recent investigations. The reports by Raup (1935, 1946) of bog vegetation in northeastern Alberta will be similarly related. Papers by Hansen (1949a, 1949b, 1952), though dealing mainly with pollen analyses of Alberta peats, contain valuable information on bog depths, nature of the peats, surface features and general bog development. The main conclusions based on peat pollens are presented elsewhere in this review.

Picea mariana ASSOCIATIONS. Forests dominated by black spruce exhibit a number of phases and intergrade with certain other kinds of vegetation. Two main types are recognized in northern Alberta; (*a*) black spruce–feather moss association, which intergrades locally with the white spruce association; (*b*) black spruce–bog moss association, regarded as a sub-climax stage of a *Sphagnum* bog sere (Moss, 1953b). " Though these associations have many species in common, including the same dominant, they do show significant differences in floristic composition; moreover, they are unlike in respect to internal structure and generally in substratum, origin, and development ".

The black spruce–feather moss (*Picea mariana–Hylocomium splendens*) association is frequently accompanied by white spruce, aspen and willows. The floor is carpeted with " feather " mosses. Associated species include lichens (*Peltigera aphthosa* and *Cladonia* spp.), *Ledum groenlandicum, Vaccinium vitis-idaea* var. *minus, Rosa* spp., *Ribes* spp., *Equisetum* spp., *Cornus canadensis, Petasites palmatus, Linnaea borealis* var. *americana, Mitella nuda, Rubus pubescens* and *Carex* spp. This association seems generally to have developed on shallow depressions or on level terrain through sedge-grass-willow stages and without much peat formation. It is similar floristically to the " mature bog forest " described for central Alberta by Lewis et al. (1928), and somewhat like the dry phase of the bog forest reported by Raup (1946) for northeastern Alberta. Moss suggests that the black spruce-feather moss association may be interpreted as an edaphic climax, being long maintained as such by poor drainage and also by periodic burning.

The black spruce–peat moss (*Picea mariana–Sphagnum*) association frequently has tamarack, paper birch and certain willows associated with the spruce. The floor is characterized by bog mosses, especially *Sphagnum* spp., and by *Cladonia* spp. The chief flowering plants are *Ledum groenlandicum, Vaccinium vitis-idaea* var. *minus, Rubus chamaemorus* and *Smilacina trifolia*. The most striking structural feature is the uneven floor of *Sphagnum* mounds and the nearly continuous cover of Labrador tea. This association has arisen in depressions through acid bog stages and with the production of a considerable thickness of *Sphagnum* peat. It is interpreted as a subclimax community, maintained as such by prevailing edaphic conditions and by periodic burning. Natural succession is to a black spruce–feather moss community; but this trend is quite generally off-set by burning which causes retrogression to earlier stages of the bog forest sere. The "young bog forest" reported by Lewis et al. (1928) for central Alberta is essentially the black spruce–bog moss association, and the wet phase of the bog forest described by Raup (1946) for the Athabasca–Great Slave Lake region is similar to this association.

Black spruce vegetation, related to the black spruce–feather moss association, is known to occur in the foothills and on the lower mountain slopes of west-central Alberta. This has been described by Horton (1954) and will be discussed in our review of Cordilleran forests. In the more northern parts of Alberta, black spruce is known to occur apart from the two associations already described (Moss, 1953a). It grows there intermixed with pine and other tree species on several kinds of terrain. On the upper slopes of the Caribou Mountains, black spruce stands and also black spruce–lodgepole pine mixtures are reported by Moss and by Raup (1946).

Drepanocladus-Carex AND *Sphagnum* BOGS. Open bogs, characterized by sparse tree cover, are of various kinds and present a number of complex problems. According to Moss (1953b), the bogs of our region fall into two main series: (*a*) *Drepanocladus-Carex* bogs, formed in basins from aquatic vegetation and marsh, and leading through bog willow and bog birch stages to a *Larix laricina* association, or through various stages to *Sphagnum-Ledum-Picea* vegetation; (*b*) *Sphagnum* bogs, developed as just indicated or from aquatic-marsh vegetation without the interpola-

tion of marked *Drepanocladus* or shrub phases. The latter mode of succession to *Sphagnum* bog has probably been the chief mode of bog development in Alberta, especially northward.   However, further investigation is needed on this as on many other aspects of our bogs.   As already indicated, open bogs tend to develop into bog forest—the *Picea mariana–Sphagnum* association.   When a bog forest is burned there is retrogression to earlier stages of the bog sere.   Certain of our open bogs, or portions of bogs, represent disclimax conditions brought about mainly through burning.   Repeated burning of relatively mature *Sphagnum* bogs tends to produce an open bog phase which is more or less static.   This is the *Ledum* moor of Lewis et al. (1928) and is characterized by Labrador tea, *Polytrichum, Cladonia,* low mounds of *Sphagnum fuscum, Eriophorum spissum, Vaccinium* spp. and scattered black spruce, paper birch and willows.

Sphagnum SUCCESSION AND THE REGENERATION CYCLE.   The ecological relationships of various species of *Sphagnum* in Alberta bogs have been discussed by Marion Moss (1949) and Moss (1953b).   In terms of leading sphagnums, succession from the early aquatic condition, through intermediate stages, to the final " xeric " stage may be shown as follows: *Sphagnum subsecundum* (or, *S. teres*) → *S. recurvum* → *S. magellanicum* → *S. capillaceum* → *S. fuscum.*   Northward in the region, *S. magellanicum* is said to be rarely represented in the sere.   This sere is clearly seen in large wet depressions of bogs, and also where sphagnum is advancing upon marsh or *Drepanocladus* bog.

The " Regeneration Complex ", described by various European writers, has been discussed for Alberta bogs by Moss (1953b). This is the condition of a growing sphagnum bog where the majority of the hummocks are covered by the more xerophilous (or, less hygrophilous) species of the sere, and where the hollows are occupied by relatively hygrophilous species.   The aspect is a mosaic of hummocks and hollows occupied by different species, and the development is cyclic, the hollows becoming the sites of mounds, and the mounds the sites of hollows, through a series of *Sphagnum* sequences.   The state of dynamic equilibrium inherent in the cycle is followed, sooner or later, by a condition of static equilibrium, viz., when the general surface of the bog has become

too dry for any of the sphagnums except *S. fuscum*. It is to be noted that the " Regeneration Complex " shows the same sequence of sphagnums as in the *Sphagnum* sere, except that the strictly aquatic species do not occur in the former.

Larix laricina ASSOCIATION. This type of vegetation, recognized some years ago in central Alberta by Lewis et al. (1928), has been described recently for more northern areas by Moss (1953b). Structurally the association has a single tree dominant, the tamarack (larch), often with black spruce interspersed; a shrub layer, usually of bog birch and willows; an uneven floor with scattered pools and with wet, mossy mats or mounds; associated with the mosses, low, creeping shrubs (*Vaccinium* spp.), small sedges and several broad-leaved herbs; occurring sporadically are low, erect shrubs, tall herbaceous plants, and coarse horsetails (*Equisetum*), grasses and sedges. The chief mosses are *Aulacomnium palustre, Camptothecium nitens, Drepanocladus* spp. and *Sphagnum* spp. Prominent herbs include *Caltha palustris, Galium labradoricum, G. trifidum, Rubus acaulis, Carex disperma, Carex* spp., *Calamagrostis* spp., *Equisetum fluviatile*, and *Potentilla palustris*.

Though dominated by tamarack, this association is ecologically and floristically similar to the black spruce–peat moss association. " Like the latter, it develops on a peaty substratum, as a subclimax stage of a bog sere, and has a floor of peat-forming mosses. The main differences relate to the fact that the tamarack establishes in a *Drepanocladus-Carex-Betula* bog which continues in a relatively wet condition. *Sphagnum* mosses often invade this type of bog, developing there along with the tamarack. The extent of *Sphagnum* development is affected by the size of the bog, by periodic flooding, and by burning. With the growth of *Sphagnum* mounds, conditions become more favorable for black spruce and ericads but less suited to tamarack, sedges, and certain other plants of the tamarack vegetation " (Moss, 1953b). As Beeftink (1951) points out, tamarack is very intolerant of shade and can not succeed in competition with Labrador tea and other plants that soon cover the enlarging *Sphagnum* mounds, while black spruce flourishes under these conditions. Thus succession to the black spruce–peat moss association may take place. Following this, in turn, there may be a succession to the black spruce–feather moss association.

MOUNDED BOGS WITH ICE CORES. Brief reference may be made to a report (Moss, 1953b) of Alberta bogs with large mounds or ridges and alternating depressions, the elevated areas remaining frozen throughout the summer, while the depressions thaw out to the bog floor. Previous reports of mounded bogs with persisting ice cores (Palsa bogs) for the Boreal Region of North America are those of Wenner (1947) and Hustich (1939, 1950) in the forest-tundra region of Labrador. Hustich suggests that this type of bog may form the southern limit of the real permafrost region. The mounded bogs of northwestern Alberta are either within or close to the permafrost zone as depicted by Muller (1947). The conditions under which " Palsa " mounds are produced and maintained are discussed briefly by Moss in the light of Hanson's (1950) experience with solifluction and mound areas in Alaska.

This discovery of permafrost areas is of interest in connection with Hansen's discussion of bog origin and persistence in central Alberta. Though Hansen (1952) encountered no permafrost in these bogs, he believes that permafrost was actually necessary for their development, at least those formed on flat terrain. It is suggested that growth of *Sphagnum* was made possible in a semi-arid region by a high watertable held up by permafrost. Hansen further suggests that " amelioration of the climate to a degree that would eliminate the permafrost also would possibly result in the extinction of many muskegs formed on flat terrain ".

Balsam Fir Vegetation

Halliday and Brown (1943) show balsam fir (*Abies balsamea*) as extending westward as far as north-central Alberta, where it is said to be of only light population intensity and restricted to moist forest habitats. It is most commonly found in mixed stands, with white spruce and poplar, in river valleys and round some of the lakes (Halliday, 1937). Confusion prevails as to the identity of the fir west of the Athabasca River, in central Alberta, for example, at Lesser Slave Lake. Halliday and Brown show the alpine fir (*A. lasiocarpa*) as extending northeastward into this region. The need of a critical study of the ranges of these fir species in Alberta and of the question of intergrading between them has been pointed out (Moss, 1953a). A recent study reported by Moss indicates that the fir at Battle Lake, some 50 miles southwest of Edmonton,

may be assigned to *Abies lasiocarpa,* though some of the trees approach *A. balsamea* rather closely. The balsam fir at Lesser Slave Lake is said (Moss, 1953) to occur generally in mixed stands with white spruce, aspen, balsam poplar and white birch, only locally in pure stands. Accompanying species are those commonly found in the white spruce and poplar associations of the region. An interesting associated species is the devil's-club (*Oplopanax horridus*). The ecological relationships of balsam fir in our region await critical study.

<div align="center">PINE VEGETATION</div>

One of the characteristic trees of the Boreal Forest, especially on sandy sites, is the jack pine (*Pinus banksiana*). This species extends westward, in northern Alberta, approximately to the line (Fig. 1) separating the Boreal and Boreal-Cordilleran regions. Associated with jack pine, in western Alberta, is lodgepole pine (*P. contorta* var. *latifolia*), a leading tree of the Rocky Mountains that has extended considerably farther east than most other Cordilleran species. The eastern boundary of lodgepole pine in northern Alberta is approximately the line between the Boreal and Boreal-Cordilleran, but in central Alberta this boundary lies much farther east to include areas near Lesser Slave Lake and close to Edmonton. Thus in the region between Edmonton and the Peace River, the ranges of these two pine species overlap. This situation, set forth clearly by Halliday and Brown (1943), has been further studied by Moss (1949, 1953a) who proposes minor changes in the boundary lines and presents evidence that many of the pines in the transition and overlapping regions are hybrids. It should be noted, too, that outliers of lodgepole pine occur still farther to the east, notably on the Caribou Mountains and the Cypress Hills. The intrusion of the lodgepole pine into the Boreal Region, the overlapping of ranges of the two pine species and the occurrence of intergrading pines serve to complicate efforts to classify the vegetation, whether in terms of phytogeographic zones or plant communities. These complexities suggest numerous intriguing and as yet unsolved botanical problems.

An effort has been made by Moss (1953a) to classify and characterize the pine vegetation of northwestern Alberta and to correlate this study with the pioneer work of Dowding (1929)

on jack pine in central Alberta and with the description by Raup (1946) of pine vegetation in the Wood Buffalo Park and near Lake Athabasca. The pine vegetation of these areas described by Raup differs significantly from pine communities elsewhere in Alberta, so far as reports indicate. Raup describes the jack pine vegetation of his region in two phases—that on sandy plains or ridges, and that on rocky hills. The former phase is somewhat like jack pine farther south but differs in several important respects, principally in its primary species, *Picca mariana, Cladonia rangiferina* and *Cetraria nivalis*.

Pinus banksiana–P. contorta ASSOCIATION. The pine vegetation in the greater part of our Boreal Region is probably best treated as one community and given the status of an association (Moss, 1953a). Within this association, two consociations may be recognized, the jack pine and lodgepole consociations, on the basis of species dominance. For each of the consociations a number of faciations may be distinguished by their ground cover. Two of these faciations are quite prevalent and rather well defined; (a) *pine–feather moss faciation,* on the more moist and more shaded sites, characterized by *Hylocomium splendens* and *Calliergonella schreberi,* along with various higher plants such as *Linnaea, Pyrola* spp., and *Cornus canadensis;* (b) *pine-heath faciation,* on the drier and more open parts of stands, characterized by *Arctostaphylos uva-ursi, Vaccinium vitis-idaea, Elymus innovatus, Oryzopsis pungens, Polytrichum* spp. and *Cladonia* spp. Common to both faciations are several species, including *Alnus crispa, Rosa* spp., *Salix* spp. and *Maianthemum canadense*.

ECOLOGICAL RELATIONSHIPS. "As is well known, jack and lodgepole pines are fire trees, commonly reproducing by seed following burning of stands. Since they are also light-demanding, they succeed on burned areas because their early growth is much faster than that of any spruce that may have started. Moreover, they send their taplike roots deep into sand and gravelly soils, making for success on apparently dry sites " (Moss, 1953a). The drier pine areas, such as tops and south-facing slopes of sand ridges, are generally occupied by the pine-heath faciation or by a treeless vegetation that may be called a " pine-heath associes ". This has a large proportion of *Polytrichum piliferum, Cladonia* spp., small

grasses and sedges, as well as numerous broadleaved xerophytes. Produced by severe burning, this associes, through pine regeneration, may develop into the pine association. However, since both drought and burning militate against the success of the pine on these drier areas, the pine-heath associes tends to persist indefinitely as an edaphic climax. On more moist pine sites, where the pine-feather moss faciation tends to become climax, pine regeneration is generally good after burning and the pine community is restored. However, with prolonged absence of burning, succession to white spruce may occur.

The " pine-moss association " described by Dowding (1929) for xeric jack pine sites on sandhills of central Alberta is similar to the pine-heath associes. Dowding's " pine-heath association " of mesic sandhill sites resembles the pine-heath faciation. Where sandhill bases and bog margins merge, the vegetation consists of a highly variable mixture of pine and bog communities. Though Dowding describes this as a " pine-birch association ", it is perhaps best treated simply as transition vegetation.

CORDILLERAN FORESTS

BOREAL-CORDILLERAN TRANSITION

The broad transition zone which we have designated the Boreal-Cordilleran Region presents difficulties to the reviewer, partly because of the inherent complexity of the vegetation and partly because this vegetation has received relatively little critical study. The poplar vegetation of southwestern Alberta has already been discussed; that of the more northern foothills and mountain areas relates to pine and spruce vegetation presently to be considered. As already noted, white spruce extends through the Boreal-Cordilleran into the Subalpine and Montane regions, where it grows at the lower elevations, merging there with Engelmann spruce. Black spruce occurs not only in the bogs but to some extent on foothill and mountain slopes as far south as the Nordegg region. The role of black spruce will be discussed in connection with our presentation of spruce and lodgepole pine forests. Douglas fir and limber pine are of some significance, especially in the Montane Forest. Lodgepole pine, already noted as prominent in the western part of the Boreal, is the chief pioneering and dominant subclimax species in the Boreal-Cordilleran and Cordilleran regions. Alpine

fir becomes increasingly prevalent westward in the foothill-mountain transition region. This species and Engelmann spruce dominate in the climax association of the Subalpine Region.

In the following summary of available information on the chief types of forest vegetation in the Boreal-Cordilleran and Cordilleran regions, the reviewer leans heavily upon a recent unpublished report by Horton (1954). Permission to quote from Horton's excellent report is acknowledged below.

WHITE SPRUCE VEGETATION

On account of the gradual transition from white spruce to Engelmann spruce in the foothills and mountains, it is difficult, if not impossible, to draw a sharp boundary line between them. Moreover, certain of the published reports make no attempt to distinguish between the two species. This is unfortunate because the altitudinal occurrence of these trees indicates considerable difference in ecological amplitude. White spruce is reported by Halliday (1937) as one of the chief species of the Foothills Section between 3,000 and 5,000 feet elevations. Clarke and Cowan (1945), in amplifying their statement that white spruce and Engelmann spruce may be taken to separate the Boreal and Subalpine forests, outline the western limits of the former species in the region of Banff National Park. White spruce is said to extend in tongues up the main valleys, for example, up the Spray River to the upper falls, up the Bow to about Eldon, and up the North Saskatchewan to the forks. West of these points the valleys are occupied by Engelmann spruce. Eastward the valleys and lower slopes and also dry slopes at higher elevations have white spruce, when they have any spruce at all. Moist sites at higher elevations have Engelmann spruce and there is a considerable area of hybridization. An earlier report for the Banff region by Lewis (1923) states that the Engelmann spruce zone does not descend much below 6,800 feet and rises in places to nearly 8,000 feet. Lewis (1917) says that white spruce near Banff occupies marshy flats in the Bow valley and covers rocky slopes between 4,500 and 7,000 feet. Horton (1954) reports that Engelmann spruce (or an intermediate form) is the characteristic spruce in the Cordilleran forests, and typical white spruce in the foothills (Boreal-Cordilleran) region.

For an area in the mountains of southwestern Alberta, Cormack (1949) says that white spruce is the chief tree, though Engelmann spruce has been reported for the region. In discussing forest cover for the general " East Slope " region of Alberta, Cormack (1953) states that " White spruce is regarded as the climax tree species for this region, where it extends from almost timberline downwards for about three thousand feet ". This statement, it must be pointed out, conflicts with the generally accepted opinion (as summarized in the preceding paragraph) that Engelmann spruce is the climax spruce species in timberline forest and in a broad zone well below timberline.

Apparently a white spruce association for the Boreal-Cordilleran region has not been recognized as such; yet data provided by Cormack (1949, 1953) and Horton (1954) seem to warrant this classification. Assuming the spruce vegetation described by Cormack for the lower slopes and the valleys to be dominated by white spruce (the upper slopes most likely by Engelmann spruce), and bringing to bear Horton's account and the reviewer's personal knowledge of the region, it becomes possible to make a rough synthesis in terms of a vegetational type or association. Cormack (1949) has provided an excellent general description of the virgin spruce forest along the Carbondale River and also a lengthy list of the species, with an indication of their relative abundance. While the proposed *Picea glauca* association occurs in several phases or faciations, the most prevalent climax phase is envisaged as follows: a dense stand of spruce, 100 to 130 feet tall and 15 to 30 inches d.b.h., and associated smaller trees of alpine fir; small tree and shrub strata, highly variable in nature, including *Salix* spp., *Cornus stolonifera, Lonicera involucrata, Viburnum edule* and *Vaccinium* spp.; herb strata, rather rich in species but quite variable and generally sparse, characterized by *Linnaea borealis* var *americana, Cornus canadensis, Equisetum arvense. E. scirpoides, Mitella nuda, Petasites palmatus, Pyrola* spp., *Thalictrum* spp., *Carex* spp., *Habenaria* spp., *Osmorhiza obtusa, Smilacina* spp., *Actaea rubra* and *Lycopodium annotinum;* a rich deep floor carpet of " feather " mosses, especially *Hylocomium splendens, Ptilium crista-castrensis* and *Calliergonella schreberi,* with scattered lichens, mostly *Peltigera aphthosa.*

It will be noted that this association differs significantly from

the *Picea glauca* association of central and northern Alberta in having alpine fir as a leading constituent. However, the fir appears to be absent from certain situations, especially some of the river valley flats. Other phases of the present association are quite divergent in respect to the lesser flora, notably a phase that seems to be peculiar to the Montane Region, and well shown in the Carbondale area described by Cormack. Characteristic of this phase are *Rubus parviflorus, Clintonia uniflora, Disporum oreganum* and *Elymus glaucus,* also a rather rich fern flora. A second important variation of this white spruce association occurs chiefly in moist valley sites of the foothills, northward in our region, and is characterized by a strong black spruce element. Successional phenomena involving white spruce of the mountains will be dealt with later in this review.

Lodgepole Pine Vegetation

Lodgepole pine has been aptly described by Clarke and Cowan (1945) as a "temporary fire type running through all forest divisions and not diagnostic of any". Horton (1954) emphasizes the complicated picture presented by the lodgepole pine vegetation of the foothills and mountains. There are certain obvious correlations between the lesser flora and site, as also between this flora and pine stocking. Under open and/or dry conditions, prevailing species with the pine include *Arctostaphylos uva-ursi, Juniperus* spp., *Zygadenus elegans, Hedysarum* spp., *Antennaria* spp. and *Cladonia* spp. Open stocking in all but the extreme sites generally produces a luxuriant growth of grasses, especially *Elymus innovatus* and *Calamagrostis* spp., and such herbs as *Fragaria glauca.* In mesic well-stocked stands the "feather" mosses generally predominate, with a variety of shrubs and herbs, for the most part *Ledum groenlandicum, Vaccinium membranaceum, V. scoparium, Lonicera involucrata, Viburnum edule, Cornus canadensis, Petasites palmatus* and *Equisetum* spp.

Horton discusses the possibility of recognizing a lodgepole pine association under the name: *Pinus-Picea-Vaccinium–Elymus–Linnaea–Feather moss–Peltigera.* However, considering the wide variations related to density of pine stands, as well as the many regional and local habitat variations, also considering the dynamic nature of succession, he prefers to adopt the "continuum" concept

as expressed by Brown and Curtis (1952). Accordingly the general subclimax pattern, presented by our lodgepole pine forests, is looked upon by Horton as a vegetational " continuum ". This is conceived of as " a continually varying series of species sorting along an environmental gradient mainly controlled by the vegetation itself ". Horton says the most important interaction relates to succession which is dependent primarily on fire.

Lodgepole Pine to Spruce-Fir Climax

Succession from lodgepole pine to a spruce-fir climax vegetation has long been recognized by ecologists as a highly significant development in the Rocky Mountains. Recent discussions on the subject by Bloomberg (1950), Cormack (1953) and Horton (1954) have served to focus attention on certain vital issues, both theoretical and practical. The first two of these writers do not distinguish between white spruce and Engelmann spruce in their presentation. Horton differentiates between succession in the High Foothills, where white spruce-alpine fir is the climax, and succession in the Subalpine Region, where Engelmann spruce-alpine fir is climactic. He also discusses the trends for xeric, mesic and moist sites. However, Horton believes that the two spruce species are similar in their successional characteristics. These investigators are in general agreement that lodgepole pine expands to subclimax dominance through the frequency of burning and that succession to a spruce-fir forest takes place. But they are at variance in respect to certain important details concerning succession itself and also the stability and permanency of the spruce-fir association. The latter question is an integral part of the larger subject and will be included in the following discussion.

EARLY STAGES IN SUCCESSION. Cormack (1953) recognizes two general successional trends, each originating in a recent burn: (a) pine and spruce to climax; (b) pine to climax. In a, spruce and occasionally fir start off at approximately the same time as pine; in b, the earlier stages are characterized by either open or dense stands of pine, with spruce entering later. Of four stages recognized for trend a, the first two are designated *Ceratodon-Parmelia-Epilobium* and *Hypnum-Peltigera-Linnaea*, these stages being named after the most characteristic species of the ground vegetation. Corresponding stages of trend b are *Ceratodon-Parmelia*

and *Hypnum-Cladonia-Vaccinium.* Associated with *Ceratodon* and *Parmelia* spp., in the early stages, are said to be *Cladonia* spp. and hair-cap mosses as well as various herbaceous flowering plants. Incidentally the report of species of *Parmelia* as characteristic crustose lichens, in a hard ground cover for our region, comes as a surprise to the reviewer. Cormack admits that his proposed scheme is an arbitrary one. That it may be so regarded is supported by Horton's (1954) extensive investigation. The wide variations in ground flora of young pine stands, depending on density of stand and the nature of the site (reported above), as well as on various effects of repeated fires and burning intensity, present an exceedingly complex picture.

VARIATIONS IN LATER STAGES. For both " trends " recognized by Cormack, the last two successional stages are the same, viz., *Hypnum-Peltigera* and *Mnium-Clintonia-Menziesia,* the latter denoting the characteristic ground vegetation of the climax forest. Cormack lists numerous herbs and shrubs that comprise the relatively rich flora of this Forest. Horton states that Cormack's findings, though attributed to the whole " east slope " or Saskatchewan River drainage, apply, according to his observations, only to the Montane and the southern portion of the Subalpine region.

Significant aspects of succession reported by Horton may be noted here. The spruce species and alpine fir depend on topographical refugia from fire for their seed source. Such residual patches are common in the rough terrain of the region. There are relatively few pine stands without some degree of spruce understory. In the vicinity of a seed supply, the spruce may form a continuous layer along with alpine fir. Distribution and abundance of spruce in pine stands depend on proximity of a seed source, and on favorable site and competition (pine density). In general, most spruce become established under pine over an age range of 10 to 40 years following fire. Thus in old stands the spruce is predominantly even-aged or practically so. Spruce is initially slow-growing, but dominants reach the pine canopy between 70 and 160 years, generally in about 125 years. " From that time spruce waxes and pine wanes ". Lodgepole pine has a maximum lifespan of 250–300 years. Dominant spruce trees usually live to well over 300 years. The maximum age found by Horton was

450 years. The rate of succession depends on the abundance and developmental rate of the tolerant species. Pine appears to prevail longer under such adverse conditions as dry sites and heavy stocking. Light ground fires and other conditions which permit pine reproduction in an old stand tend also to lengthen the sere. The duration of the sere seems to vary from 225 to 375 years. Black spruce is of some importance on lower slopes, northward from the Nordegg district. From bog refugia it extends into upland pine stands. It becomes established over a variable initial age range and may continue to reproduce thereafter by layerings. Usually it remains suppressed during its life-span which seldom exceeds 200 years. Aspen competes favorably with conifers only in localized protected sites of the mountains and higher foothills. In the lower foothills it is more successful, but even there it may be succeeded by pine in one generation. However, it is favored by burning because of its ability to propagate by suckering.

NATURE OF THE SPRUCE-FIR CLIMAX. For mountain slope forests near Blairmore, Bloomberg (1950) reports that lodgepole pine regenerated thickly on burns, stagnated at 150 years and was gradually succeeded by spruce to produce spruce-fir stands of great age and apparent stability. Remarkable, however, is the absence of any preparation on the part of apparently climax stands to perpetuate themselves, for spruce regeneration is said to be " conspicuous by its scarcity " and fir regeneration hardly profuse enough to fill in sparse gaps. Bloomberg furnishes evidence that the age-class distribution in these stands is directly attributable to fire and that without periodic burning the climax type tends to become decadent. He says fire is not only associated with the succession cycle leading to the establishment of the spruce-fir complex " but is actually the kingpin of the whole structure "; and " without fire in such proportions as to be catastrophic from a protection point of view there would be no valuable forests to protect ". Cormack (1953) emphasizes the stability of the climax spruce-fir forest and gives an account of regeneration differing from that suggested by Bloomberg. He states that " reproduction and subsequent growth of spruce and fir occurs under openings in the forest canopy due to the windthrow of overmature trees " and that " large numbers of spruce and fir seedlings may be found growing on almost every moss-covered windfall ".

Horton (1954) states that there is great variation in spruce and fir content in different climax stands and prefers to conceive of the climax as " a variable pattern ". Different aspects of this variable spruce-fir climax are discussed. Horton found several stands where alpine fir was increasing rapidly and spruce on the wane. Despite its short life-span of about 200 years, fir has certain advantages over spruce, viz., its greater tolerance and its capacity to reproduce prolifically by both seed and layering. For these reasons alpine fir may be regarded as the culminating species. On the other hand, fir is greatly retarded by various factors, especially browsing by large game animals. Horton inclines to the view that where fir is kept down through browsing or other agencies, spruce will predominate. He says that spruce does continue to reproduce, though sparingly, in openings of the climax stand. Incidentally he agrees with various other investigators that spruce seedlings rarely become established in the dense moss mat of the forest floor, but often on rotten, fallen, fire-killed timber. Though Horton reaches no definite conclusion as to the permanency of the spruce-fir climax forest, he seems to agree with Bloomberg that this is actually an academic question. While alpine fir may well be regarded as a theoretical climax, fire is so frequent in the region that a forest is not likely to survive long enough for the fir to gain general dominance over spruce, a period of somewhat over 500 years being envisaged.

Picea engelmanni–Abies lasiocarpa ASSOCIATION

A comprehensive description of this association in Alberta has yet to be published. Nevertheless, data supplied by Cormack (1949, 1953) and by Horton (1954), as well as the reviewer's personal knowledge, make possible a brief account of its salient features. Actually the more important aspects, those pertaining to dominant species, general development and equilibrium, have been discussed above. It remains to indicate the internal structure and floristic composition of the association. For the following brief and rather tentative description, the present writer must assume the major responsibility.

Under the forest canopy formed by the two dominant trees, *Picea engelmanni* and *Abies lasiocarpa,* a few small tree species and large shrubs occur more or less sporadically. These include

Salix spp., *Alnus* spp. and *Sorbus scopulina*. Smaller shrubs are generally more prevalent—*Vaccinium membranaceum*, *V. caespitosum*, *Viburnum edule*, *Ribes lacustre*, *Rosa* spp., *Lonicera* spp., *Spiraea lucida*, *Rhododendron albiflorum*. Woody species restricted to the more southern parts of the region are *Acer douglasii* and *Ribes viscosissimum*. Certain of those common in the south (Montane Region) also extend northward but do not reach the more northern parts of our forest, e.g., *Menziesia glabella* and *Vaccinium scopulorum*. Still others are found mainly northward, e.g., *Vaccinium vitis-idaea* and *Empetrum nigrum*. On the basis of minor woody species alone, two or more faciations of the association are indicated. Herb strata, for the association as a whole, include species of *Equisetum*, *Carex*, *Juncus*, *Luzula*, *Habenaria*, *Smilacina*, *Saxifraga*, *Thalictrum*, *Viola*, *Ranunculus*, *Mitella*, *Pyrola*, *Osmorhiza*, *Epilobium*, *Fragaria*, *Castilleja*, *Linnaea borealis* var. *americana*, *Cornus canadensis*, *Parnassia fimbriata*, *Trollius albicaulis*, *Galium triflorum*, *Pedicularis bracteosa*, *Erigeron salsuginosus*, *Arnica cordifolia*, *Streptopus amplexifolius*, *Zygadenus elegans*, *Lycopodium annotinum* and various ferns and grasses. Important additions for the south of Alberta are *Clintonia uniflora*, *Xerophyllum tenax* and *Elymus glaucus*. Species that seem to appear only northward in the association include *Rubus pubescens* and *R. pedatus*. There is a rich ground cover composed chiefly of " feather " mosses, including the three species listed for most other coniferous woods in Alberta and species of *Rhytidiadelphus*, also species of *Mnium* and many others. Liverworts and lichens are prevalent in the moss carpet, especially the large lichen, *Peltigera aphthosa*. Mosses and lichens also cover windfalls and lower trunks of trees. It may be added that the *Picea engelmanni-Abies lasiocarpa* association of Alberta appears to be richer in species and less homogeneous than is the corresponding association, described recently by Oosting and Reed (1952), in the Medicine Bow Mountains in Wyoming. As these authors suggest, further studies of this wide-spread subalpine community should be made.

OTHER CONIFEROUS ASSOCIATIONS

The Montane Forest, as it occurs in Alberta, is generally said to be characterized by Douglas fir, lodgepole pine, Engelmann spruce and white spruce, with some limber pine on the foothills

and clumps of aspen at the contact with the Grassland Formation (Halliday, 1937; Moss, 1947; Horton, 1954). The very rare occurrence here of western white pine (Moss, 1944) and of ponderosa pine and western cedar (Cormack, 1949) is of considerable interest. However, as Horton points out, the Montane Forest in Alberta is recognized better by its shrub and herb species than by its tree dominants. Species peculiar to the forest are said to be *Rubus parviflorus, Ribes viscosissimum, Berberis repens,* and *Clintonia uniflora.* This Forest occurs at elevations of 4,500 to 6,500 feet in the Waterton district and extends northward to the Crowsnest Pass. Douglas fir and various of the associated species have apparently intruded from British Columbia along passes through the Rocky Mountains. Isolated stands or patches of Douglas fir occur in the Porcupine Hills, in the Bow Valley and at Jasper. Brief accounts of vegetational units dominated by Douglas fir and by limber pine have been given by Moss (1944) for rocky ridges in the park belt region lying between Waterton Lakes Park and Crowsnest Pass.

DOUGLAS FIR VEGETATION. Small stands of this tree (*Pseudotsuga taxifolia*) are said to occur locally on sandy-gravelly foothill slopes and on the better protected slopes of rocky ridges. The tops and exposed slopes of these ridges, which are subjected to strong desiccating winds, are characterized by limber pine. An interesting array of plants appears in these Douglas fir stands. A few of the species listed by Moss are: *Rubus parviflorus, Rosa* spp., *Amelanchier alnifolia, Acer douglasii, Clematis columbiana, Spiraea lucida, Lonicera glaucescens, Agropyron trachycaulum, Calamagrostis* spp., *Aster conspicuus, Erigeron speciosus, Heracleum lanatum, Glycosma occidentalis, Smilacina racemosa, Disporum trachycarpum, Hieracium griseum, Erythronium grandiflorum, Cystopteris fragilis* and *Claytonia lanceolata.*

LIMBER PINE VEGETATION. Exposed to very strong winds on the dry slopes and summits of rock ridges, the limber pine (*Pinus flexilis*) trees are generally dwarfed and distorted. Actually the pine forms an open community with many exposed areas of various sizes. Only locally do the trees provide shade and otherwise influence accompanying species. In most places the rock has weathered to form a thin loose shaly soil; elsewhere it is practically

unweathered. In spring and early summer these areas are veritable rock gardens, displaying a wealth of form and color. Of the numerous species listed by Moss for various aspects of these "pine ridges", the following are recorded here to indicate the range in life-form and flora: *Arctostaphylos uva-ursi, Juniperus horizontalis, J. sibirica, Populus tremuloides, Potentilla fruticosa, Shepherdia canadensis, Phlox alyssifolia, Physaria didymocarpa, Sedum stenopetalum, Astragalus pauciflorus, Aster conspicuus, Penstemon confertus, P. nitidus, P. eriantherus, Arabis spp., Draba spp., Townsendia parryi, Phacelia sericea, P. linearis, Polemonium pulcherrimum, Selaginella densa, Agropyron spicatum, Artemisia spp., Cryptantha bradburiana, Erigeron spp., Antennaria spp., Allium cernuum, Solidago spp., Paronychia sessiliflora, Lychnis drummondii, Hedysarum sulphurescens, Lupinus leucopsis.*

ALPINE VEGETATION

Few papers have been published on the alpine vegetation of Alberta, and these are quite limited in their scope and treatment. More has been written about similar vegetation lying to the south in the United States and that of the far northern mountains beyond Alberta (Raup, 1934, 1947a; Porsild, 1945). By interpolation one can arrive at a fairly good general understanding of our own region. A summary account of ecological aspects of Rocky Mountain alpine vegetation has already appeared (Daubenmire, 1943). Therefore the present review aims merely to sketch the salient features of our region and to correlate some of the reports that have appeared. Discussion of arctic-alpine problems, including Hultén's contribution to the phytogeography of the region, is largely excluded from this article. For comprehensive reviews of these subjects reference may be made to Raup (1941, 1947b).

Alpine vegetation occurs between timber line of the subalpine forest and snowline. For Alberta mountains as a whole, timber line varies from an altitude of 6,500 to 8,000 feet, the line being, in general, progressively higher southward. Daubenmire (1943) points out that nowhere is the youthfulness of Rocky Mountain topography more important vegetationally than in the alpine zone. "Here the surface is essentially an alternation of rocky outcrops with depressions of varying degree of imperfect drainage, and the soil, when present, varies from peat to gravels which are practically

devoid of organic matter ". The plants are said in relation to this striking edaphic heterogeneity to form communities seldom extensive or very homogeneous. As Daubenmire also reports, alpine vegetation consists almost entirely of perennials, mostly of the caespitose habit and either herbaceous or suffrutescent. The Rocky Mountain alpine flora has long been known to contain many arctic species. Gray and Hooker (1880) stated that it is an arctic flora, or rather prolongations of it southward along the mountains, with certain admixtures of species from more southerly regions. Lewis (1923) notes that many of these arctic species in our region have a circumpolar distribution, e.g., *Dryas octopetala, Silene acaulis, Sedum rhodiola, Saxifraga cernua, Oxyria digyna, Polygonum viviparum* and *Arctostaphylos alpina.* Rydberg (1914) deals with this subject for the Rocky Mountain region as a whole, and Daubenmire (1943) gives a concise summary. Briefly it may be said that our alpine flora derives from two main sources—the arctic tundra and local endemic areas. According to Rydberg, more than one-third of the alpine species of the Rockies are endemic, though several of them are apparently derived from glacial or arctic plants.

VEGETATIONAL ZONATION

The alpine vegetational formation is often divided into three zones, these being delimited, respectively, by forest (timber) line, tree line and scrub line (Lewis, 1923). Forest line is the altitudinal limit of forest grown trees. The transition from subalpine, sprucefir, forest to tree line is usually very gradual and is characterized by groves of trees and isolated individuals, the latter often stunted and distorted; hence this zone is known as " krummholz ". For the Banff region Lewis places this tension belt at about 7,200 feet. The chief tree species of this zone in our region are alpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmanni*), alpine larch (*Larix lyallii*) and white-bark pine (*Pinus albicaulis*). In the scrub zone these species become even more stunted, the main stem often creeping with short erect shoots and assuming fantastic forms. Trees of the " flag " shape grow here; also matted atoll-like rings of offspring are produced by layering. It is amongst the groves of these zones that the " alpine meadows " are found. " Of many different types according to aspect, slope of ground and amount of moisture, the vegetation here shows more diversity and

greater profusion of flowers than any other region either in the temperate or tropical belts" (Lewis, 1923). Beyond the scrub line, to the region of perpetual snow or ice, the vegetation consists of small plants, many having a circumpolar distrubution, as noted above.

CHIEF COMMUNITIES

Alpine habitats, in their great diversity, support varied and heterogeneous assemblages of plants. The following summary of the more prevalent communities is largely adapted from Lewis (1917) on the Banff region and Daubenmire's (1943) general account.

BOULDER-FIELD VEGETATION. The boulders of old moraines and rock-slides are characterized by crustose lichens and a scant flora of crevice and creeping plants, such as *Oxyria digyna, Penstemon fruticosus, Dryas octopetala, Lychnis apetala, Sibbaldia procumbens, Poa alpina* and *Salix nivalis.*

FELL-FIELD VEGETATION. Gravel areas commonly support a sparse vegetation in which low rosette and mat-forming species predominate, e.g., *Dryas octopetala, Silene acaulis, Erigeron* spp., *Polemonium* spp., and certain grasses and sedges.

ALPINE MEADOW. Occupying the more mesic habitats, and characterized by a rich and diversified flora, this so-called "meadow" may be described in two phases; (*a*) mat-grassland, with a preponderance of grasses and many early-flowering broad-leaved plants, including species of *Poa, Agrostis, Festuca, Trisetum, Potentilla, Anemone, Heuchera, Sieversia, Pedicularis,* also, *Polygonum viviparum* and *Myosotis alpestris;* (*b*) mat-herbage, dominated by herbs, with scattered grasses, the growth being less luxuriant than in the mat-grassland, including *Dryas octopetala, Sibbaldia procumbens, Saxifraga* spp., *Potentilla* spp., *Poa alpina* and *Festuca ovina.* The following type is also prominent in "alpine meadow", as this is understood by some writers.

HEATH VEGETATION. Commonly found between the groves of conifers in the transition zone, this ericaceous vegetation is characterized by *Cassiope mertensiana, C. tetragona, Phyllodoce empetriformis, P. glanduliflora, Pedicularis bracteosa* and *Saxifraga* spp.

SNOW-PATCH FLORA. Where snow remains in moist protected areas until late summer, this characteristic flora appears, the more common species being *Erythronium grandiflorum* var. *parviflorum, Anemone occidentalis, Ranunculus eschscholtzii, Valeriana sitchensis, Antennaria racemosa, Carex scirpoidea.* Some of these plants, notably *Erythronium* (snow lily), can often be seen in flower at the edge of snow-banks in August.

ALPINE BOG. This highly variable type occurs in several phases, two of which are prevalent: (*a*) sedge bog, dominated by species of *Carex*; (*b*) willow bog, dominated by shrubby willows. Associated therewith are grasses and species of *Eleocharis, Ranunculus, Caltha* and *Trollius.* Mosses are often present and there is usually a considerable accumulation of sedge or moss peat.

ENVIRONMENTAL FACTORS AND FOREST LINE

The replacement of forest by forms of alpine vegetation is doubtless brought about by the interplay of many factors, involving topography, substratum, insolation, temperature, precipitation, wind velocity, snow, burning and biological agencies. As Daubenmire (1943) points out, there is a lack of sufficient research in the way of controlled experimentation to warrant very definite conclusions concerning the relative effects of different environmental factors. Yet, certain conclusions, drawn mainly from general field observations, are indicated.

Shaw (1909) emphasizes snow, rather than wind, as the principal cause of timber lines and alpine grassland. However, his study pertained more to the Selkirks than to the Rocky Mountains. Lewis (1923) believes that wind and snow are usually the two main factors tending to limit forest growth in alpine regions of the Alberta mountains. Griggs (1938) concludes that wind, not low temperature, puts a limit to upright tree growth in these mountains. Daubenmire (1943) states that the evidence from various sources points to the conclusion that " throughout most of the Rockies the upper altitudinal limits of tree species which reach timber line are determined primarily by high wind velocity and that wind is effective by promoting transpiration at times when the soil is frozen and plants cannot absorb or conduct moisture with sufficient rapidity to replace that lost by transpiration ".

The possibility of a general shift in the timber line level of our

region during recent times has been investigated by Griggs (1938). He had previously found the forest to be invading the tundra at Kodiak in Alaska. From studies done at various points, including Glacier National Park, Lake Louise and Jasper, Griggs concludes " that in the Rocky Mountains, timberline and therefore climate is static, or more precisely, that any change which climate may be undergoing is at a rate of a different magnitude than at Kodiak, too slow to be detected by the methods employed ". Most examples of forest advance in our region, Griggs was able to explain in terms of re-invasion of ground from which forests had been removed, mostly by fire. The general conclusion reached by Griggs regarding climate is of considerable interest in connection with the prevailing idea that the mountain glaciers of our region are receding.

ALPINE PLANT SUCCESSION

Xeroseres and hydroseres have been indicated for the Alberta alpine region but no critical work has been reported. Reference may be made to investigations, such as those of Whitfield (1933) and Cox (1933) in the United States, as representing the kind of study that should be done in our region. There is one paper dealing with plant succession in the Canadian Rockies that should be mentioned here. This is by Cooper (1916) on the Mount Robson region which lies close to the British Columbia–Alberta border. Though Cooper's study deals with forest zones, rather than the alpine, it is mainly concerned with primary seres and therefore relates closely to succession under alpine conditions. Cooper says two primitive surfaces are left bare by the retreat of the ice—rock surfaces and moraines. Each of these soon generates another, so that four habitats are offered to invasion by plants; rock surfaces and talus; moraines and shingle flats.

MARSH AND-REED SWAMP VEGETATION

For our present purpose, the terminology used in a recent paper (Moss, 1953b) will be adopted. A marsh is defined as a grass-sedge-rush community, usually without mosses or much peat accumulation and the floor covered with water one or more months of the growing season. A shallow marsh, having water only a small part of the growing season, is a wet meadow. A reed swamp is a very wet marsh characterized by such plants as bulrushes

(*Scirpus*), cattails (*Typha*) and coarse grasses (e.g., *Scolochloa festucacea*). A bog is characterized by peat-forming mosses, commonly *Sphagnum,* also by ericads and conifers. Marsh-bog transition vegetation is not uncommon in our forested regions.

FRESH-WATER AREAS

Marsh and reed-swamp vegetation has been described for representative portions of forested Alberta apart from the Rocky Mountains. Concerning this vegetation in our prairie parkland region, little has been published; but a brief account for the corresponding part of Saskatchewan has appeared. Marshes and reed swamps are associated with the numerous ponds and lakes throughout much of Alberta. In general there is a gradual transition from aquatic vegetation through reed swamp to marsh on the margins of these bodies of water. Depressions without open water, and occupied by marsh, are also common. In the prairie region a marshy border of a shallow lake (slough) may be flanked by a narrow bank of willows but usually merges gradually with the prairie grassland. In the forested regions there is generally a succession of marsh to willow (sometimes with alder), followed by balsam poplar and white spruce. However, under certain conditions succession is from marsh to either *Hypnum* (*Drepanocladus*) or *Sphagnum* bog and to bog forest.

In their pioneer work on reed swamps and marshes (" low moors ") of central Alberta, Lewis et al. (1928) show these to be of diverse types and complex relationships. Only a few features will be noted here. (Emended specific names are substituted for certain of those appearing in the paper). The chief dominant species of reed swamps are *Scirpus validus, Typha latifolia, Scolochloa festucacea* and *Carex atherodes.* Common associated plants are *Sagittaria cuneata, Sparganium* spp., *Equisetum fluviatile* and *Lemna minor.* Leading dominants of marshes are *Carex aquatilis, C. rostrata, C. diandra, C. lasiocarpa, Glyceria* spp., *Calamagrostis inexpansa* and *C. canadensis.* Accompanying plants include *Alopecurus aequalis, Poa palustris, Hordeum jubatum, Beckmannia syzigachne, Eriophorum* spp., *Eleocharis palustris, Scutellaria epilobiifolia, Galium trifidum, Ranunculus sceleratus, Sium suave, Cicuta* spp., *Stellaria* spp., *Aster* spp. and *Stachys palustris* var. *pilosa.* A common sequence on borders of alkaline

sloughs is reported somewhat as follows: Aquatics → *Typha-Scirpus* → *Scolochloa–Carex atherodes* → *Glyceria–Carex* spp. → *Salix* spp. → *Populus balsamifera*. Marshes extending across wet basins appear generally to be acid (pH about 6) and are characterized by *Carex diandra, C. lasiocarpa, C. rostrata, C. aquatilis, C. chordorrhiza, Poa palustris, Eriophorum* spp., *Triglochin maritima, Equisetum fluviatile, Potentilla palustris, Menyanthes trifoliata* and a mat of *Hypnum* (*Drepanocladus* spp.) on the floor.

A somewhat similar account of marshland is given by Raup (1935) for the Peace-Athabasca delta region in northeastern Alberta. The flood-plain and delta lands have extensive marshes, ranging from aquatic shore associations to grasslands. The sloughs and wet meadows are separated by natural levees and other alluvial deposits, tenanted by willow clumps or timber. Two of the most widespread species, *Calamagrostis canadensis* and *Carex trichocarpa* var. *aristata* (*C. atherodes*), form extensive " hay meadows " throughout the lowlands. Raup describes this rather complex vegetation in some detail, including common successional trends. The main hydrarch sequences may be summarized as follows: *Potamogeton* → *Nuphar–Sagittaria–Myriophyllum* mixtures → *Scirpus–Typha–Glyceria–Eleocharis* mixtures → *Carex rostrata* (or, *Carex atherodes* → *Calamagrostis*) → *Salix planifolia* → *Salix–Alnus–Populus* mixtures → *Picea glauca*.

Meadows, wet marshes and related vegetation of the Peace River region in northwestern Alberta are described by Moss (1953b). Readers are referred to this recent paper for a list of aquatic and shore-line species and a brief account of reed swamps, marshes and wet meadows, including retrogression of marsh through burning and succession of marsh types to bog.

Only brief notes have been published on marsh vegetation in the prairie region of southeastern Alberta. Slough borders there are characterized by *Scirpus validus, S. americanus, S. paludosus, Typha latifolia, Hordeum jubatum, Beckmannia syzigachne, Alopecurus aequalis, Eleocharis palustris, E. acicularis, Carex lanuginosa, C. praegracilis, Puccinellia nuttalliana, Deschampsia caespitosa, Agrostis scabra, Iva axillaris* and species of *Juncus, Rumex, Atriplex, Chenopodium* and *Polygonum*. Less stagnant marshes found in sluggish water courses and stream flats have

extensive stands of *Polygonum coccineum* and *P. amphibium* var. *stipulaceum*. The more saline depressions often support an abundance of *Puccinellia nuttalliana, Distichlis stricta, Spartina gracilis, Salicornia rubra, Suaeda depressa, Glaux maritima, Iva axillaris, Atriplex nuttallii* and *Monolepis nuttalliana*. In the extreme south of the Province, some of the drier lowlands, such as flats of river valleys and coulee bottoms, are dominated locally by grasses (*Agropyron smithii. Distichlis stricta*), sagebrush (*Artemisia cana*) and greasewood (*Sarcobatus vermiculatus*).

SALINE MARSHES AND MEADOWS

Of considerable interest is the account by Rawson and Moore (1944) of rooted aquatic plants and lake shore species in the prairie parkland of Saskatchewan. It may safely be assumed that the lakes of the eastern prairie-parkland region of Alberta are quite similar to those described for Saskatchewan. According to Rawson and Moore, most of the lakes are shallow, with no outflow and with a high degree of salinity. The majority have from 300 to 30,000 p.p.m. of total solids. The salts are chiefly sulphates of magnesium or sodium. The pH of these lakes (mostly 7.8 to 8.9) indicates a moderately alkaline condition, " not sufficiently important to justify their local description as alkaline, rather than saline, lakes ". The more common rooted aquatic plants are reported in relation to their occurrence in lakes of varying salinities. The fennel-leaved pondweed (*Potamogeton pectinatus*) is the most widespread, ranging from fresh water to a lake with a salinity of 20,000 p.p.m. Ditchgrass (*Ruppia*) is also highly resistant to salinity. *Chara* is reported for a lake with a salinity of 7,870 p.p.m. and in all of the lakes of lesser salt content. Other species for which salinity range is shown include: *Potamogeton richardsonii, Myriophyllum spicatum, Utricularia macrorhiza, Hippuris vulgaris, Sagittaria cuneata, Potamogeton vaginatus* and *P. zosteriformis*. Plants common at or near the water's edge of these lakes include *Scirpus paludosus, Typha latifolia* and *Carex* spp. The exposed shores of the saline lakes are said to have a characteristic flora of halophytes. Those found in the more saline locations are *Salicornia rubra, Distichlis stricta, Suaeda erecta, Atriplex hastata* and *Triglochin maritima*, tending to occur in this order, progressively from the lake to less saline soils.

For parts of the Salt Plain region south and west of Fort Smith, in the northeast corner of Alberta, Raup (1935) has described a distinctly halophytic flora. The most characteristic feature of these Plains is said to be the salt marsh vegetation which grows in undrained depressions. Leading species are *Salicornia europaea, Puccinellia nuttalliana, Suaeda depressa, Spergularia salina, Plantago eriopoda, Glaux maritima, Triglochin maritima, Chenopodium rubrum, Distichlis stricta* and *Hordeum jubatum.* Somewhat similar vegetation has been described by Moss (1953b) for small saline meadows near Fort Vermilion, well northward in Alberta.

MISCELLANEOUS TYPES OF VEGETATION

BADLAND AREAS

Extensive badlands occur along the Red Deer river, especially near Drumheller and Steveville. These are famous as a source of dinosaur skeletons. Other smaller badlands are found elsewhere in southeastern Alberta. The eroded faces and banks of these areas are almost devoid of vegetation but have patches of prairie and other plants on the more favorable sites. Among the more conspicuous species are the sage-brushes (*Artemisia longifolia, A. cana*), creeping juniper (*Juniperus horizontalis*) and bearberry (*Arctostaphylos uva-ursi*). On flats between the badland hillocks, cacti (*Opuntia polyacantha, O. fragilis*) are prevalent.

PRAIRIE SANDHILLS

Contrasting sharply with the pine sandhills and ridges of central and northern Alberta are the low sandhills of the mixed prairie region, such as those lying southwest of the Cypress Hills near Lake Pakowki. These hills are in part stabilized by vegetational cover composed chiefly of the prairie grasses. Other parts are subject to active dune formation and are characterized by *Sporobolus cryptandrus, Oryzopsis hymenoides, Calamovilfa longifolia, Elymus canadensis, Cryptantha fendleri, Rumex venosus* and *Psoralea lanceolata.* Associated with these sand-loving species, certain shrubs are often found, notably *Prunus demissa, Rosa arkansana, Juniperus horizontalis, Symphoricarpos occidentalis* and *Elaeagnus argentea.* Locally willow clumps and even poplar trees are well established, presumably where the water table is fairly high. These include *Salix interior, S. bebbiana, S. amygdaloides*, aspen poplar and cottonwood (*Populus sargentii*).

The region provides a great diversity of stream courses, from rushing mountain creeks to the great rivers, the latter flowing through the forested areas or through the plains. Obviously many kinds of vegetation are supported by the waters, banks, flats, lagoons and deltas of these various streams. However, very little has been published on the subject for our region. The most comprehensive work is that of Raup (1935) for northern Alberta, especially his account of the vegetation of stream courses and river deposits in the Peace-Athabasca delta region. There is also a brief account of aquatic and marginal vegetation of creeks and rivers in the Peace River region by Moss (1953b). Poplar vegetation of river flats in the prairie parkland of southwestern Alberta has been described briefly by Moss (1944). The forested margins of the Carbondale River in the mountains of southwestern Alberta are described by Cormack (1949).

Raup's (1935) paper may be consulted for an account of some rather special topics pertaining to lagoon and delta conditions. Presented here is merely a general picture of the present writer's conception of the characteristic flora of creeks and rivers in the Boreal Region of Alberta. This is based partly on the published papers and partly on personal observations. The more sluggish waters have such submerged and emergent species as *Myriophyllum exalbescens, Sagittaria cuneata, Hippuris vulgaris, Sparganium multipedunculatum, Nuphar variegatum, Ranunculus trichophyllus, Polygonum amphibium* var. *stipulaceum, Lemna trisulca, Callitriche* spp. and *Potamogeton* spp., especially *P. richardsonii*. Stream banks and flats are characterized by *Scirpus rubrotinctus, Glyceria* spp., *Typha latifolia, Juncus alpinus, J. nodosus, Equisetum palustre, E. pratense* and *E. arvense,* also by such woody plants as *Salix interior, S. arbusculoides, S. lutea, S. planifolia, S. lasiandra, S. subcoerulea, Alnus rugosa, Cornus stolonifera, Populus balsamifera* and *Picea glauca*. Less prominent plants include: *Poa palustris, Carex rostrata, Cinna latifolia, Parnassia palustris* var. *neogaea, Achillea sibirica, Sium suave, Epilobium glandulosum* var. *adenocaulon, Erigeron philadelphicus, E. lonchophyllus* and *Stachys palustris* var. *pilosa*. Where balsam poplar and white spruce dominate near the water's edge, as they commonly do, the herbs and shrubs of these associations generally form a luxuriant

growth.   Streams flowing through marsh or bog usually have various sedge species along their banks.

Flats of rivers in the prairie parkland of southwestern Alberta are commonly dominated by poplars and willows, with which are associated birch, alder and a variable assemblage of herbaceous species (Moss, 1944).   The leading poplar species are *Populus angustifolia, P. acuminata, P. sargentii, P. trichocarpa* (near the Mountains) and *P. balsamifera*.   There is said to be evidence of hybridization between certain of the cottonwoods and also between the two balsam poplars.   The chief willows are *Salix lutea, S. caudata, S. interior* var. *pedicellata, S. melanopsis* and *S. amygdaloides*.

Virgin coniferous forest along the Carbondale River in the mountains of southwestern Alberta is well described by Cormack (1949) in his study of trout streamside cover.   Spruce is the chief tree on the banks of the river and on the river flats.   " On the immediate banks, often overhanging the water, willow and alders, together with a number of other small trees and shrubs, fill in the intervening spaces between the tall spruce ".   The most constant feature is the luxuriant, continuous moss carpet over soil, boulders and windfalls.   Near the river margin the mossy, overhanging banks are tenanted by various shade-loving shrubs, ferns, horsetails, sedges and broad-leaved flowering plants.   (See our review of spruce vegetation).

CALCAREOUS BOGS

A small number of these unique bogs is known to occur in south central Alberta, near Edmonton.   They are associated either with *Sphagnum* bogs in shallow depressions or with spruce-poplar woods on flats below a valley slope.   Apparently lime-charged water from springs seeps in slowly to produce conditions suitable for an unusual kind of bog development and a characteristic flora. The surface of the bog consists of peaty mounds and shallow pools of water, the bottoms of the pools being whitish with marl deposit. The mounds, which are of various shapes and size, support a mixed vegetation, generally with mats and cushions of small mosses and scattered herbs, shrubs and small trees.   Unfortunately the bryophytic flora has not been studied.   Intermixed with the mosses, the little club-moss *Selaginella selaginoides* is often found.

Turner (1949) has listed the chief herbaceous and woody species for one of these bogs. Leading herbs are *Tofieldia glutinosa, Triglochin maritima, Allium schoenoprasum* var. *sibiricum, Carex viridula, Juncus longistylis, Dodecatheon pauciflorum, Lobelia kalmii, Gentiana macounii (G. tonsa), Pinguicula vulgaris* and *Antennaria pulcherrima*. Bog birch is usually present; also willows, including *Salix candida* and *S. glauca* var. *glabrescens*. Small trees of *Betula papyrifera, Larix laricina* and *Picea* spp. often become established on the larger hummocks.

MOUNTAIN PEAT BOGS

Sphagnum bogs, though prevalent in our northern foothills, are apparently rather uncommon in the mountains. In any case they have not been described. Nor have other bog-like areas of the Alberta mountains received much attention. One rather common type, the " hangmoor ", has been studied to some extent by foresters. Crossley (1951) gives a brief account of this interesting formation, with particular reference to the soil. He says hangmoor peats are found on gentle slopes where the ground water, being held up by the relatively impervious nature of the till, passes through them horizontally. The vegetational cover is said to be predominantly sedge, commonly with a fairly dense cover of dwarf birch, with some willow and a sparse stand of spruce. The hangmoor merits further study.

APPLIED ECOLOGY AND CONSERVATION

This review has thus far referred only briefly to certain practical problems relating to our vegetation, such as overgrazing of prairie grassland and regeneration of desirable timber stands. Even under the present heading there is no intention of dealing in any comprehensive way with the application of ecological principles to problems of utilization and conservation of vegetational resources. It is proposed only to draw attention to a few of the major issues pertaining to the utilization of our two main types of vegetation, prairie and forest, and to indicate how these issues are currently being regarded by administrators and by investigators.

RANGE PROBLEMS

It is perhaps fitting to refer first to the problem of providing suitable range for " the monarch of the plains ", the bison (buffalo). The main bison herd, now located in Wood Buffalo Park, includes

not only the northern or wood bison but also a large element of the plains bison, the latter having been moved there several years ago from a Reserve in south-central Alberta. In his studies on range conditions in Wood Buffalo Park, Raup (1933, 1935b) emphasizes that sedge sloughs provide the main food supply for the bison, especially during the winter. He notes that the problem of winter feed seems to be the critical one for bison in the north. Soper (1941, 1951, 1952) has written a comprehensive account of the northern bison and has also reported on the flora and fauna, including the plains buffalo, as currently found in Elk Island Park, near Edmonton. Banfield's (1947) bulletin on the mammals of Waterton Lakes National Park includes a discussion of range conditions there. Several reports, some in mimeographed form, have been issued by Cowan (1952) and others on grazing and browsing conditions for wildlife in the Rocky Mountains.

Critical studies of our native pasture lands commenced in 1927 with the establishment of the Dominion Range Experiment Station, the first institution of its kind in Canada, near Manyberries in southeastern Alberta. Important work has been done on the botanical composition, carrying capacity and utilization of ranges and on the chemical composition of native forage plants (Clarke et al., 1930 to 1945). Research under the Federal Department of Agriculture is continuing in Alberta, that relating to the foothills ranching region being now directed from the Experimental Station, Lethbridge. University botanists, whose papers on prairie vegetation are reviewed above, have made significant contributions, as also has Hanson (1951, 1952, 1953) in his work with the Eastern Rockies Conservation Board. These various studies have helped to provide a scientific basis for advising ranchers regarding their ranges and for the framing of policy pertaining to the classification and utilization of areas.

FOREST PROBLEMS

Until recently forestry officials in our region have devoted their attention almost exclusively to the administration of timber lands and to the most insistent of all forest problems, that of burning. Even so, forest fires have been rampant and have taken tremendous toll. However, it is hoped that, with improved facilities being provided, forest fires will be located more quickly and controlled

more effectively in the future. Until recently only a few ecological studies have been carried out by foresters in Alberta. Of these, studies on forest site indicators by Holman (1929), Parker's (1942) work on site criteria and Halliday's (1937) classification of forests may be mentioned.

Within the last few years the outlook has changed considerably. In 1949 the Alberta Government launched a survey of the Province's forest resources, with a view to the preparation of forest inventories and cover maps. Since 1951 the Canadian Government has been participating in this program which combines air photography and mapping with the study of sample areas by ground crews. Alberta foresters have also been showing an active interest in ecological research. Bloomberg (1950) reaches the conclusion that fire has a positive and causative effect on the establishment of spruce as a climax type, and poses the interesting question: " What will be the state of affairs when the ideal of complete fire protection is realized? ". Assisted by the Alberta Department of Lands and Forests, Cormack (1949, 1953), University botanist, has carried out several studies of mountain vegetation in relation to stream flow, watershed protection, strip mining and forest succession. The Federal Government has greatly expanded its forest research facilities during recent years. In Alberta, ecological studies on different forest types have been initiated, for example, the study by Horton (1954) on the ecology of lodgepole pine (already reviewed at some length). Attention is being given to forest soils (Crossley, 1951) and to regeneration of desirable forests on denuded or poorly stocked areas (Crossley, 1952). The Federal Government has also established in Alberta a laboratory for research in forest biology, especially investigations of insects and diseases affecting forest trees; and good results are already coming from this centre. " The most notable post-war development in Alberta has been the establishment of the Eastern Rockies Conservation Board. This joint board, supported by the Federal and Provincial Governments, is charged with responsibility for protecting the eastern slopes of the Rocky Mountains, in which rise the headwaters of the Saskatchewan River and its tributaries "—quoted from " Canada's Forests, 1946–1950 ", Department of Resources and Development, Ottawa, 1952. This reference introduces the final section of the present review.

Watershed Problems

Particular reference is to be made here to Alberta's great watershed, the east slope of the Rocky Mountains. It should be noted, however, that watershed problems exist in many other parts of Alberta, and especially in agricultural areas. Attention is directed to an excellent bulletin by Toogood and Newton (1950) on water erosion in Alberta.

Concerning the watershed of the Saskatchewan River, commonly known as " The Eastern Slopes ", it has been authoritatively stated that " the dominant interest in this area, particularly from the federal standpoint may be said to be the regulating effect of forest cover on the flow of streams originating within the watershed " (Kennedy, 1948). The main responsibilities of the Board (to which reference has been made above) are briefly as follows: to provide projects and facilities required for the conservation of the forests and the protection of the watersheds in the area; to protect the forests of the area from fire, etc.; to conserve, develop, maintain the forests in the area with a view to obtaining the greatest possible flow of water in the Saskatchewan River and its tributaries.

During the past five years there has been much discussion on this important project. Complex natural phenomena are being investigated and attempts must also be made to resolve conflicting human interests. The main objective of watershed control may seem to conflict with one or more of several desirable uses of the region, such as: production of high-grade timber; bountiful supply of trout and big game; summer grazing for domesticated animals; aesthetic and recreational purposes. Of particular interest to ecologists is the stress the Board places on the " multiple-use " concept. The aim appears to be three-fold—to maintain the watershed in its original condition or better, to ensure optimum use of all resources in perpetuity, and to co-ordinate the various uses. One of the more contentious problems, that of grazing use of forest lands, has been discussed by Hanson (1952). He maintains that properly managed grazing fits nicely into a multiple-use land management where watershed value holds a place of prime importance.

In a comprehensive discussion of the Board's views on multiple forest use, Fellows (1952) emphasizes that water yield is the prime

concern and that the season at which water is available may be just as important as the total annual flow. Along with the growing demand for water, there is apprehension over the possibility of a diminishing supply. " The great glaciers of the Rockies, which contribute substantially to the summer flow of many of the larger streams, have been shrinking steadily for a number of years. In effect, this means that these streams are drawing on capital reserves of moisture rather than on the current snowfall and rainfall alone. Eventually this source of water may become almost negligible, and a compensating supply must be found elsewhere ". Fellows goes on to discuss the effects of logging, grazing, fire, mining operations, game management, water erosion, forest cover, etc. "As to the most desirable kind of forest cover needed to promote the maximum water yield, much yet remains to be learned ". Special studies are being made on stream flow in relation to precipitation, on the capacity of soil mantle and surface rock to absorb rainfall and snow-melt and to store moisture. Fellows discusses the view that a watershed should, as far as possible, be maintained in a primeval condition, since in that state it probably provided a good, and well regulated, supply of clear water. The Board's problem, however, is to induce nature to release more water from the catchment area. To achieve this, " nature must be coaxed and not bullied ". " If the latter approach is used, nature will surely revolt and the last state will be worse than the first ". The underlying argument put forward by Fellows is that, " where high water-yield is the primary objective, it is probable that the concept of the multiple-use of forests has a better chance of adoption than under any other conditions ".

ACKNOWLEDGMENTS

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THE BOTANICAL REVIEW

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INTRODUCTION

The genus *Arceuthobium* (Loranthaceae) is one of the most extraordinary genera of flowering plants as well as one of economic importance, for many of its members, commonly known as " dwarf mistletoes ", are significant pathogens of timber trees. Botanically it is distinguished by many uncommon, if not unique, features. Among these may be mentioned the nature of the endophytic system, the female and male flowers, the complexity of the fruit and the ability to induce the formation of witches' brooms on hosts. Economically the damage done by these parasites to many forest trees, especially in western North America, exceeds that of almost any other single cause, with the possible exception of heart-rotting fungi.

It is therefore surprising to find that many of the species have been quite inadequately studied. It is with the possibility of future studies in mind that the present literature review of the genus is attempted.

The writer has collected in excess of 400 references on dwarf mistletoes. For the present, however, only those references were abstracted which, in the writer's opinion, make a definite contribution to a wider knowledge of the dwarf mistletoes. Only these

are listed in the " Literature Cited ". Furthermore, and largely because of the unsettled state of classification within the genus, a taxonomic treatment is deferred to a later date, although an outline is indicated in the contents. For a taxonomic treatment of the North American species, the reader is referred to Gill (1935).

MORPHOLOGY AND ANATOMY
Endophytic System

The part of the mistletoe plant developing within the host tissues has been variously named, the particular term used in each case depending upon the writer's idea as to its homology. Thus it has been called a system of rhizomes (von Schrenk, 1900), roots (Heil, 1923; Peirce, 1905; Weir, 1916a), thallus (Heinricher, 1923), and finally the endophytic system (Thoday and Johnson, 1930).

Peirce (1905) considered the endophytic system homologous to a true root, originating from a true but modified radicle. From this standpoint he regarded the formation of a shoot as " an instance of regeneration without wounding, amputation or other pathological stimulus ". In his view, " the small part of the seedling which penetrates the host forms and develops stem and leaves, a small part of one organ—the root—develops into a complete plant by forming the missing members ".

Heinricher (1923), after a series of morphological studies on *Arceuthobium oxycedri*, finally rejected the morphological concept of a root in *Arceuthobium* altogether. He regarded the entire plant as the direct outgrowth of the hypocotyl, neither radicle nor plumule being differentiated in the seedling. Although he believed the endophytic system to be analogous to a root system in function, he thought it more comparable to the mycelium of a fungus, and designated the endophytic system as thalloid. This term, however, is certainly not satisfactory for various reasons, e.g., tracheary elements are present. In view of the lack of agreement as to terminology, the writer prefers to use the non-committal term " endophytic system " suggested by Thoday and Johnson (1930).

The method of entrance of the " haustorium " and the advance of the endophytic system in the host tissues have been matters of considerable debate. The presence of mechanical force is generally agreed upon. There has been some question as to the possibility

of enzymatic action.   Heinricher (1923) thus comes to the con-
clusion that penetration takes place almost exclusively by a forcing
aside of the host cells, although he still considers the possibility of
secretion of pectase for dissolution of the middle lamellae.   Thoday
and Johnson (1930) believe that cells of young invading strands
have the ability to secrete a wall-softening enzyme, possibly a
pectase.   Heil (1923) states that cells of the endophytic system
dissolve the walls of the host cells, while stone cells are enclosed
and digested.   Peirce (1905) also speaks of dissolution of host
cells by haustorial cells of the parasite.

The anatomy of the endophytic system defies adequate descrip-
tion.   The direction of growth of mistletoe strands appears com-
pletely erratic except in wood rays, the direction of which is
adopted by invading parasitic strands, and in cases where a leaf
trace may be followed for a short distance.   The young strands
are simple filaments of somewhat elongated cells filled with dense
protoplasm, each with a large conspicuous nucleus.   These fila-
ments branch freely and irregularly, often anastomosing in the
manner of a fungous mycelium.   The youngest part of the endo-
phytic system contains a stainable substance which later increases
slightly in amount.   Heinricher (1923) believed this substance to
be chlorophyll, but Heil (1923) interpreted it as an oil.   These
opinions are not necessarily contradictions, since these workers
studied different species on different hosts.   The remarkable speed
of growth of young strands is mentioned by several workers.
Thoday and Johnson (1930) found slender strands to within two
millimeters of the shoot apex of the host branch in August; the
parasitic strands thus seem to keep pace with host elongation.   It
is probable, however, that the rate and general direction of growth
differ from species to species, and perhaps also depend on the
species of host involved.   *Arceuthobium douglasii, A. pusillum*
and frequently *A. americanum* seem to grow toward the tips of
host branches only, while members of the *campylopodum-vagina-
tum* complex are able to grow in both directions.   These differ-
ences in behavior are believed by Gill (1935) to be linked more
with the host species than with inherited characters of the
mistletoes.

In due course the cells of the young uniseriate strands undergo
divisions, at least the first two of which are longitudinal (Thoday

and Johnson, 1930). Thus a series of tiers of four cells each frequently results. During further development a cylinder of cells is formed, the inner cells of which soon begin to differentiate into tracheary elements. The entire process, however, is quite irregular. A continuously functioning cambial layer as well as indications of phloem tissues seem completely absent. Before the cortical strands have fully matured, the first young radial sinkers are already present in the wood.

Observers generally agree that no true phloem is present in either stem or endophytic system of *Arceuthobium*, although the parenchyma surrounding the xylem elements in the latter could be interpreted to represent phloem tissues (Dufrénoy, 1936). Peirce (1905) found this parenchyma in contact with the cells of the host phloem. The association of the xylem tissues of host and parasite has been interpreted variously. Cohen (1954) could observe no direct contact between the xylem elements of *Pinus ponderosa* and those of *A. campylopodum*. Johnson (1888), however, who worked with *A. oxycedri* on *Juniperus* sp., believed that the walls of the host tracheids were separated along the middle lamella through penetration by the parasite. The thin-walled parasitic cells would thus be brought into intimate contact with the host tracheids. Dufrénoy (1936) observed extreme fragmentation of the vacuoles of cells in contact between the two organisms, and accepted this as evidence of active translocation of nutrients.

The gross anatomy of the endophytic system is also characterized by its complexity. Two main types of strands may nevertheless be recognized, cortical strands and sinkers (Solms-Laubach, 1867). The cortical strands occur in the tissues external to the cambium. They have essentially the protostelic features as described above. The sinkers develop endogenously (in *A. campylopodum*) from cortical strands (Cohen, 1954). After penetrating the sheath of the cortical strand, a young sinker, which does not have the tiered arrangement of a young cortical strand, grows centripetally, and usually contiguous to one of the numerous uniseriate phloem rays of the host, until the cambium is reached. No cambium cells appear to be destroyed by the invading strand. A pathological stimulus, however, seems present, causing the cambium to initiate locally a ray which differs markedly in appearance from

both the normal uniseriate rays and fusiform rays containing resin canals. This aberrant ray is formed around the young sinker, which gradually becomes embedded. The embedded sinker constitutes the innermost part of the endophytic system, and seems to maintain a more or less constant position. Scalariform tracheary elements are differentiated in the central zone of the sinkers, but in a very irregular fashion and, according to Heil (1923), not infrequently in contact with host tissues. Clusters of pits form a lattice-like pattern on the side walls of the parenchyma cells of the sinker. Two to several of the aberrant rays may coalesce and form a single large, fusiform, aberrant ray. Within such a compound ray, the original groups of tracheary elements usually remain distinct.

An interesting question is how, or whether, the cortical strands retain their relative position and connection with the sinkers under the constant pressure of newly formed host cells. The distance between the cortical portion of the endophytic system and the sinkers must become greater with time because of the phloem and xylem cells produced by the host. Cohen (1954) suggested some possible explanations for the ability of the mistletoe to cope with this situation. First of all, host cells may, when under pressure, glide past the relatively stationary cortical strands. Secondly, new strands and sinkers may be formed continuously by the inner part of the endophytic system, the large outer strands being discarded with the bark. Cohen also observed some intercalary addition of cells at the base of the sinker which may accommodate the increasing tension in the sinker. It is unlikely that there is any radial movement of the sinkers, for Heil (1923) found a certain coincidence of wall topography in contiguous host and parasite cells: the bordered pits of the host were situated opposite the unthickened parts of the mistletoe xylem elements in the cases where these cells were in contact. The same writer also noted that the cortical strands were not situated parallel to the cambial cylinder of the host, but gradually approached this at their tips. This again could be interpreted to mean that the centrifugal movement of the cortical strands at the oldest part of the infection had been initiated.

The largest cortical strands fuse and separate as irregularly as the youngest filaments. Thoday and Johnson (1930), however,

found two well-developed tendencies in *A. pusillum* on *Picea*. On branches from witches' brooms, the end of each year's growth showed a large number of cortical strands. A cluster of aerial shoots was often present here. Also, at the base of other aerial shoots there was a convergence of strands.

The place of formation of an aerial shoot can first be recognized by a slight swelling on the outer side of one of the largest strands. The tiered arrangement of cells within the strand is lost soon afterwards. The fact that buds always arise on the outside of strands may be attributed to the influence of light. The formation of a bud may be considered analogous to the origin of an adventitious bud upon a root.

Whether the endophytic system is for any length of time dependent upon the aerial parts of the parasite is a question of some interest. Gill (1935) states that strong evidence exists that old infections of *A. vaginatum* and *A. campylopodum* may become systemic in character. They may live for some years within that part of the host where thickness of the bark prevents emergence of shoots, without visible evidence of their presence, until its growth reaches a younger part where profuse fruiting may take place.

Stem and Leaves

A young stem consists of a series of conspicuously articulated segments placed end to end. The basal portion of a segment is usually four-angled; the terminal portion an expanded rounded rim with the vestiges of two decussately arranged scale-leaves that are often indistinguishable from the segment proper. The tendency for roundness of the stems is more marked in some species than in others (Gill, 1935), the taxonomic significance of this is not fully known. Very old basal segments of some species are almost cylindrical, but their shape seems to be a response, in part, to the amount of moisture in the shoot.

The size of the shoot differs greatly between and to some extent within species. Shoots range from a few millimeters (*A. minutissimum*; Gorrie, 1929) and a few centimeters (*A. douglasii, A. pusillum*) up to ten and 15 centimeters (*A. vaginatum, A. campylopodum, A. americanum*; Gill, 1935). While the smaller species can frequently be identified in this way, size alone is unreliable for identi-

fication in the larger species. Thickness of shoots varies similarly, only some smaller species, for example, *A. douglasii,* being readily distinguished by very slender branches. The ratio of length to diameter of segments seems to hold some promise as a segregating character, although this ratio often differs between basal and terminal segments on one shoot. Elongation of the young segment is maintained for several months by intercalary growth; periodic increases in the length of the shoot are effected through the activity of terminal and lateral buds.

Stem color varies from very dark purplish-brown in *A. pusillum* through yellow to bright green in *A. campylopodum.* Eames (1903) found recognizable differences in both color and shape between plants of *A. pusillum* on spruce and tamarack. Other authors suggest that the color of the stem is influenced by such variables as light, temperature and latitude. It is also possible that the physiological state of the host has some effect in this connection (Gill, 1935).

It is only in the larger dwarf mistletoes that branching occurs regularly, though occasionally primary side branches are formed in *A. douglasii,* and rarely so in *A. pusillum.* Two main types of branching may be recognized: verticillate, as in *A. americanum,* and branching in a fan-like manner, as in *A. campylopodum* (Gill, 1935).

The anatomy of the stem is distinct from that of the rest of the Loranthaceae. The arrangement of vascular bundles is to some extent dependent upon the position and age of the section studied (Gill, 1935). In a young fully elongated segment there is one central cylinder of vascular tissue in the middle of the segment, running out into two distinct masses at the distal and proximal ends. With increasing age the number of strands becomes greater and their distribution more scattered. Spiral thickenings make the vessel elements particularly conspicuous. No true phloem has been found, but in old stems there may be a narrow band of thin-walled cells in such a relation to the xylem bundle as to suggest a collateral ectophloic bundle. In young stems even this indication is apparently absent.

The vascular bundles are embedded in a parenchymatous sheath bounded by an uniseriate epidermis. The cells of the sheath retain considerable meristematic qualities. Thus they may pro-

duce, often without much regularity, vascular tissues, strands of sclerenchyma and nests of sclereids. Normal cork is absent from the stems, except where wound cork has been formed.

In young stems a one-layered epidermis is present with stomata, the axes of which are at right angles to the long direction of the stem. The latter feature is likely a result of the intercalary growth already mentioned, and is also found in the other mistletoes. With age, this original epidermis is gradually replaced by a secondary cuticularized layer (Damm, 1901) which is a product of the outer cortical cells. An old shoot, therefore, is supplied with a perennial epidermis-like layer without lenticels or stomata.

The distribution of shoots on host branches may be separated into two general types, although one species, *A. americanum,* may show both types of behavior, even on the same tree (Gill, 1935). Shoots may arise in tufts from small localized centers, as is commonly the case in *A. campylopodum,* or they may be fairly regularly distributed along the length of young branches, which is the rule in *A. pusillum.* The latter has been described by Jack (1900) and Pomerleau (1941). The last year's growth of branches of a mistletoe broom on spruce were found to be without external evidence of the parasite. The second last year's growth showed small buttons of one to two millimeters; the preceding year bore the first shoots and pre-formed flowers. Four-year-old growth supported fruiting branches, after which few shoots were present. Thoday and Johnson (1930) offered a similar description but pointed out the frequent clustering of stems toward the end of the year's growth. This has also been noted for *A. douglasii* (Tubeuf, 1919). Gill (1935) believes that the distribution of mistletoe stems over host branches is primarily a function of the host.

Mention of sterile shoots of dwarf mistletoes is contained in several places in the literature. Johnson (1888), however, found no purely vegetative shoots. Later, Gill (1935) confirmed this when he found " no plants . . . in which all ramifications of the stem were not potentially able to produce at least one crop of flowers. In fact, the shoot has become so expressly modified for reproductive purposes that it might very well be regarded as an inflorescence ".

The result of isolated observations without study of the complete life cycle is strikingly illustrated by the inconsistency of the

references to the longevity of dwarf mistletoe shoots. Thus Peirce (1905) and Korstian and Long (1922) believe that shoots of *A. campylopodum* die and are dropped after seed discharge and flowering in female and male plants, respectively. Heinricher (1918) believes the above authors to be incorrect and suggests that insect attack may be responsible. The longevity of the shoots, however, seems to be different for many species. In *A. minutissimum*, shoots are annual (Gorrie, 1929); those of *A. pusillum* are practically biennial (Jack, 1900), attaining their full size in one season, flowering and fruiting in the next, after which they fall away. Dowding (1929) believes that the aerial shoots of *A. americanum* survive several years and produce several crops of flowers. Heinricher (1918) believes the same to be true for *A. oxycedri*. For the remaining species no accurate observations are available. A simple approach to this problem was suggested by Heinricher who noted secondary growth in basal segments of *A. oxycedri* (although no regular annual rings were observed) as evidence of the age of the shoot. It should be relatively simple to apply this method to other species.

As already mentioned, the vestigial leaves can hardly be distinguished from the remainder of the segment. Their arrangement is decussate, and their shape varies from slightly to markedly cuspidate, the slight notches between them sometimes becoming fairly deep sinuses. These features become increasingly obscure with age (Gill, 1935). The stomata, epidermis and cuticle of the leaves seem little different from those of the stem, although Tubeuf (1919) ascribes to the stomata a more active participation in respiration.

Male Flowers

The genus shows some pronounced differences in the time of flowering. No reference regarding the flowering time of any of the Asiatic species could be found. The flowering time of the European *A. oxycedri* has been variously stated as April to May (Klekovski et al., 1869) and August to September (Willkomm et Lange, 1870). Heinricher (1915c) offered as solution for this apparent contradiction the suggestion that the flowering time in this species is not definitely restricted, so that single flowers may occur

throughout the year.   A distinct maximum was found, however, in September and August.

The North American species can readily be divided into two main groups, one containing those species flowering in spring and early summer, the other consisting of those species flowering in late summer and fall.   In the first group belong *A. americanum, A. douglasii* and *A. pusillum.*   The *A. campylopodum*-complex makes up the second group.   The remaining species, *A. vaginatum,* seems somewhat more indefinite in its flowering time, but has a maximum in May and June (Gill, 1935).   It is interesting that the latter species is currently separated from *A. campylopodum* only by a two- or three-months difference in flowering time, no consistent morphological differences having been discovered.

Although, again, data from the Asiatic species are lacking, the remaining species show a remarkable uniformity in the morphology of the male flower.   If any differences are present they are in degree, not in form, and of no diagnostic value.   This seems to apply equally well to the size and shape of individual structures and to color of the flower.

The buds of male flowers share this uniformity to an equal extent, with the solitary exception of the pedicelled habit which seems restricted to *A. americanum* and *A. douglasii* (Gill, 1935), in the latter of which it is rare.   The color of the buds varies within the same limits as that of the stem, their shape being dependent to some extent on the position on the shoot.   Terminal buds are often globose, those formed in the axils frequently flattened, especially in *A. campylopodum.*

The gross structure of the mature male flowers is extremely simple.   Each consists of one whorl which is usually 3-partite, occasionally 4-partite, rarely 2- or 5-partite, each segment bearing a single sessile anther, and joining below a slight elevation of the receptacle, usually termed the " central cushion ".   From the writer's experience it seems likely that the proportion of 3- and 4-partite flowers may differ between certain species, particularly between *A. campylopodum* and *A. americanum* [3].   This was also

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[3] It is of some interest that Mason (1934) also noted a high proportion of 4-partite flowers in fossil dwarf mistletoes from the Pleistocene, which were referred to *A. campylopodum.*

suggested by Dowding (1931a) who detected only 4-partite flowers on branches of *A. campylopodum* f. *tsugensis*. Gill (1935), however, states that this can be found in all species.

The shape of the perianth lobes varies from broadly to narrowly or acutely ovate, and from flat to boat-shaped. Their shape is somewhat influenced by the partition, and by position of the flower; terminal flowers are usually more regular. The color of the lobes ranges from greenish to straw color and bright yellow, but may be subject to environmental influences. The entire perianth is shed after flowering.

The nature of the anther alone places the genus *Arceuthobium* in a unique position in all angiosperms. In no other flowering plant does the archesporium of the anther take the form of a continuous ring of tissue around a sterile column. This fact was not at first recognized, and the anther was described simply as bilocular or unilocular. Heinricher (1915b) suggested that these different interpretations may be based on sections which did or did not go through the central columella, respectively. Although no evidence in favor of this idea was found, the same author nevertheless believed that the continuous archesporium may be the result of fusion of four locules. Dowding (1931a), however, working on *A. americanum,* found considerable support for Heinricher's views. The columella in this species is quite variable. It may divide the anther almost completely into two sacs; it may disappear half way up, a new partition arising at right angles; or partitions may give out branches extending to the anther wall. These partitions tend to divide the single archesporium into four parts, and are present in every degree of incompleteness. The anthers of the remaining species have unfortunately not yet been studied.

The archesporium is surrounded first by a tapetal layer, next by two layers of one cell thick each. The outer or epidermal layer, according to Dowding (1931a), becomes the fibrous layer, which is another unique feature of the genus.

Complete agreement prevails among workers on various species regarding the absence of vascular bundles leading to the anthers, which are almost completely sessile. To quote Johnson (1888): " The single vascular bundle of the perianth segment on which the stamen occurs makes a slight bend towards the stamen beneath its insertion, and one or two of the vessels may point a little

towards it, but there is no indication of an independent vascular supply in the stamen ". It is interesting to mention the observations of the same author on the development of the stamen. The position of a stamen in a very young flower was found to be quite different from that in an expanded flower. The stamen arises as a multicellular lateral outgrowth of the floral axis, independent of the perianth segment, and acquires its final position by intercalation of the lower half of the perianth segment as a belt of tissue common to the stamen and perianth segment.

The structure usually called the " central cushion " is a mass of undifferentiated cells drawn out in corners alternating with the perianth lobes. It has been interpreted as a rudimentary pistil by Eichler (1878), which view was rejected by Heinricher (1915b). As support for Eichler's belief, Dowding (1931a) found numerous pairs of glandular cells on the central cushion of A. americanum, suggesting nectaries. It is of interest to note that in some species of a closely related family, the Santalaceae, a very similar central cushion exists.

Dehiscence of the anther is by an irregular circular slit. The pollen, when fresh, is bright yellow. Although Dowding (1931a) mentions the red color of pollen in A. americanum, the color in all material seen by the present writer was bright yellow. Individual pollen grains are sphaeroid, with three spinulose lobes separated by three smooth grooves which converge at the poles. Gill (1935) recognized differences in size and shape between specimens. Furthermore, the grains of A. pusillum seemed to be consistently larger than those of other species.

Chromosomal work has been done on young anthers only; the results, however scanty, merit mention. Pisek (1924) reports that meiosis in A. oxycedri was often interrupted because of physiological difficulties in the nutrition of the parasite; irregularities in the distribution of chromosomes to the tetrad cells may occur, leading to degeneration of pollen in many anthers. According to this author, a relation between the occasional shift in chromosome numbers and pathological difficulties may possibly exist. Diploid and haploid chromosome numbers of this species are believed to be 26 and 13. In other respects, meiosis agreed with that of Viscum; sex chromosomes were not distinguishable in either of these species. Dowding (1931a) found meiosis in A. americanum to occur in

late July, the chromosome number of this dwarf mistletoe being $n = 14$. From material examined by the present writer, this would seem to take place in the middle of August, although this difference may be the result of geographical and seasonal variation. No cytogenetical work has been attempted on any of the remaining species.

Female Flowers

The same uniformity of morphology characteristic of the male flower prevails in the female blossom in all species of *Arceuthobium* studied. Again, data on the Asiatic species are completely absent [4], and so only the female flower of the European and some New World species can be discussed.

A mature flower is a small elliptic structure of the same color as the shoot, and in some species hardly protruding from it (Heinricher, 1915*b*). The perianth consists of two, rarely three, lobes which are almost entirely fused with on another and with the pistil, the style of which is slightly longer than the perianth segments. Within the ovary a single locule contains an undifferentiated mass of tissue, the ovarian papilla, embracing the two embryo sacs.

Thus the morphology of the pistillate flower is such that it does not open in the manner of the male flower. This renders it extremely difficult to judge the length of the flowering season by the female flower alone. It is probably safer to accept as criterion for the flowering time of a species that of nearby male plants (all dwarf mistletoes are dioecious). In contrast to the latter, the flower of the female plant is not shed, but the entire floral organ develops into the fruit.

The 2-partite condition of the pistillate blossom is an important generic character, but in at least two instances 3-partite flowers have been recorded (Gill, 1935). Several shoots of 3-partite pistillate flowers have been found of *A. vaginatum* on *Pinus leiophylla*. Perianth segments of these were bright orange, somewhat divergent from the pistil and united for only half their length. One instance where a trimerous flower had developed into a fruit has been reported from *A. pusillum*. The rarity of these cases,

[4] Datta in 1951 described a highly unusual flower of *A. minutissimum*. This flower was bisexual and 2-partite; the ovary completely superior instead of inferior; and the stigma trifid. These features are so extraordinary that, in the opinion of the present writer, this flower can hardly be interpreted until the floral morphology of this species is better known.

however, still allows the maintenance of the 2-partite conditions as a generic character.

The extreme simplicity of the female flower is in striking contrast to the complexity of the fruit developing from it. The base of each perianth segment is invaded by a vascular strand which branches in a fan-like manner and nearly reaches the tip. Smith and Smith (1943) considered some of these traces to be " recurrent ", and from this inferred the inferior ovary in *Arceuthobium* to be of receptacular origin. The carpels, on the contrary, are entirely evascular and are fused with the perianth segments to such a degree that only a very short style and stigma emerge from the mouth-like opening of the perianth. In *A. americanum* the stigma is unequally bilobed. On the basis of shallow indentations in the stigma of this species, Dowding (1931*a*) considered the ovary to consist of four carpels which fuse in varying degrees, in two's and three's. According to this interpretation, three carpels are commonly fused completely, the fourth incompletely, although all four may be fused occasionally, forming a complete rim. No evidence supporting this theory has been put forward for other species. Thoday and Johnson (1930) found slender septate hairs on the stigma of *A. pusillum,* even after shrivelling up of this organ; this has not been reported for other species.

From the stigma an obscurely funnel-form stylar canal, entire or two- to four-lobed, leads down to the single locule. The epidermis of this canal is covered by a thin cuticle. The stigmatic exudations observed by Dowding (1931*b*) and Heinricher (1915*b*) on *A. americanum* and *A. oxycedri,* respectively, are believed to originate in this epidermis. Heinricher thought the exudate of the European species to be a fatty oil, emerging through the stomata of a definite region of the stylar canal. Later this drop would be withdrawn into the flower, simultaneously drawing pollen grains caught in the drop into the stylar canal. If Heinricher's interpretation is correct, another unique feature is added to those of the dwarf mistletoes, for oil as a secretion of the stigma or as a receptive fluid for pollen grains is not known from any other Angiosperms.

The embryo sacs are embedded in a terminal outgrowth of the floral axis consisting of undifferentiated parenchyma enclosed in a columnar epidermis. No suggestion of integuments is present.

By this feature, i.e., the absence of true ovules, the Loranthaceae are separated from the Santalaceae which have a single erect ovule. Within the ovarian papilla the two embryo sacs are situated toward the apex and near the surface. The fact that these embryo sacs alternate with the four carpels, as distinguished by her, led Dowding (1931a) to believe that "the four outer carpels are sterile and bear only stigmas, while the embryo sacs are borne on an inner whorl of orthogonally arranged carpel rudiments". This belief was sustained by the fact that four, not two, groups of archesporial cells are first present in the young ovarian papilla, these groups alternating with the four carpels recognized by the same author. The gynoecium would therefore be represented by: $G = 4 + 4$.

According to this hypothesis, the ovarian papilla would be a fusion of four rudimentary elements. This, however, is opposed to the view of Johnson (1888) who believed the ovarian papilla to be "a placenta formed of the modified apical part of the floral axis bearing two imbedded ovules reduced to their simplest condition". Bancroft (1935) also rejected the theory of carpel polymorphism. It must furthermore be kept in mind that the hypothesis of Dowding is entirely based on her interpretation of the stigma of one species, and that no other species have as yet been studied in this respect.

Pollination, Fertilization, Embryology

From the description of the pollen grains of *Arceuthobium* it may be seen that they are more typical of entomophilous than of anemophilous plants. A thorough consideration was given to both possibilities by Heinricher (1915b). The only feature which the dwarf mistletoes have in common with many anemophilous plants is the inconspicuousness of the flowers, especially the pistillate ones. Other features usually associated with this type of pollination are completely absent. On the other hand, several entomophilous features are present, among which may be mentioned the sessile anthers, the moderate amount of pollen produced, the spinulose nature of the pollen, making it cling together in balls, and the presence of a stigmatic secretion. Heinricher (1916) found that few berries were produced on plants kept in a greenhouse and concluded that, although insects probably play the most important role in pollination, both types of pollination can occur in nature. Weir

(1915) observed hymenopterous insects taking part in pollination, while the writer has seen ants visiting flowers of male plants of *A. americanum.*

The time elapsing between pollination and fertilization seems to be different for several species. Johnson (1888) found in *A. oxycedri* (presumably flowering in the fall) that the pollen grains sent a thin pollen tube down the stylar canal, which penetrated the ovarian papilla at its summit and passed in for some distance toward the apices of the embryo sacs; then it became dormant until the next spring, when fertilization took place. Dowding (1931*b*), however, observed fertilization taking place a few days after pollination of *A. americanum,* a spring-flowering species. This must occur also in *A. pusillum,* where production of fruit takes place in the same season as pollination. At any rate, macroscopic changes occur in all spring-flowering species directly after pollination, while in all others there is no apparent development until the following spring. Development of the fruit, however, is not always dependent upon fertilization, since fully developed fruits without a trace of embryo or endosperm are not infrequently found (Gill, 1935).

Development of the embryo sac seems to follow the usual pattern in angiosperms. Johnson (1888) saw several intermediate stages leading to the mature embryo sac which, as has been pointed out, is completely embedded in the tissue of the ovarian papilla. Knowledge of the developing embryo is only fragmentary. Thoday and Johnson (1930) believed that no suspensor is formed in *Arceuthobium;* this is also the case in *Viscum.* Nevertheless they did observe a haustorial extension thrust down by the developing embryo into the base of the ovarian papilla. The entire ovarian papilla is pushed aside by the enlarging endosperm and after a few months is to be detected below it. The mature embryo is extremely simple and will be further described in the following section.

In several places in the literature on *Arceuthobium* the occurrence of polyembryony is mentioned. It is false polyembryony, since the two " seeds " are produced by two embryo sacs of independent origin (see Webber, 1940). Peirce (1905) first found two embryos within a single " seed " of *A. campylopodum,* but they were of unequal size, and only one could have developed into

a new plant. Johnson (1888) had previously been unable to find polyembryony in *A. oxycedri*. Weir (1914) observed two embryos in one " seed " in *A. americanum, A. douglasii* and *A. vaginatum* f. *cryptopodum*. No information on the occurrence of polyembryony in any of the other species is available.

Mature Fruit: Dispersal Mechanism and Subsequent Germination of the " Seed "

Because of the selective nature of the present treatment, the large amount of detailed information on the fruit available from several papers cannot be included. The following is based on Gill (1935). For more detailed information and specific differences, the reader is referred to Johnson (1888) and Heinricher (1915c) on *A. oxycedri,* to MacDougal (1899) on *A. vaginatum* f. *cryptopodum* and to Peirce (1905) on *A. campylopodum* f. *campylopodum*.

Fruits have been described accurately for only a few species. In general the mature fruit ranges in color from blue to olive green. It is a fleshy, ovoid to oblong structure, attached to the shoot by a recurved pedicel. A striking feature in the genus is that the upper and lower parts of the fruit are invariably of different shades, separated sharply by an equatorial line. Despite the fact that a number of older species, now reduced to synonymy in many cases, were said to be distinguishable on fruit characters, more careful observations appear to indicate that these have little specific diagnostic value (Gill, 1935).

Anatomically the fruit consists of a highly specialized and differentiated pericarp, enclosing an otherwise naked endosperm and embryo. Below the equatorial line the exocarp consists of a thinly cutinized epidermis without stomata. This overlies a layer of parenchyma consisting of irregularly shaped living cells with slightly thickened secondary walls and interspersed with conspicuous intercellular spaces. This layer, which resembles the spongy parenchyma of some leaves, is eight to ten cells thick in the mature fruit. It extends from the equatorial line to the dehiscent layer at the base of the fruit. Inside this spongy tissue is a layer of parenchyma composed of relatively thick-walled, closely packed cells. As pointed out above, the spongy layer ends at the equatorial line, where it is replaced by the sclerenchyma sheath. The epidermis over this sheath is heavily cutinized and provided with stomata.

The only vascular tissues in the fruit are two strands of primary xylem, one median in each perianth segment.

A sheath of mucilaginous cells, dome-like above, encloses the " seed ". The cells of this mucilaginous layer, which is thought to correspond to the mesocarp, are elongated, the ends being firmly attached to the exocarp and endocarp. Johnson (1888) found these cells to be filled with viscin, developed through dissolution of the originally extremely thick cell walls.

The endocarp is represented by a sheath of large, angular, thin-walled cells without intercellular spaces. At maturity these cells are crushed, forming an envelope around, but never attached to, the endosperm and embryo.

The straight cylindrical embryo lies in the longitudinal axis of an ovoid mass of endosperm. As pointed out above, true ovules are not present in this genus; consequently we can not speak of seeds as such. The embryo consists of an undifferentiated mass of cells covered by a one-celled columnar epidermal layer, and is slightly notched at the cotyledonary end, but otherwise entire. As Tubeuf (1923) has shown, the radicle is slightly exserted from the endosperm; it lacks a root cap and is distinctly green.

Lack of agreement between authors indicates that the mechanics of the explosive dehiscence of the fruit is still not completely understood. For the present, Heinricher's (1915c) and Johnson's (1888) descriptions are followed, but for other interpretations the reader is again referred to the authors mentioned above.

The existence of considerable pressure as the propelling force of the " seed " is, of course, undeniable. Heinricher considered this pressure to be built up in the mucilaginous layer through imbibition of water by the slime threads. He further inferred that the parenchyma layer acted as a water storage tissue for this purpose. At maturity the pressure built up in the fruit is so great that the pericarp gives way at the dehiscent layer at the base of the fruit. The dehiscent zone is torn horizontally, the elasticity of the stretched pericarp comes into play, and the oblong tapering " seed " is shot out through the base of the fruit, often for a distance of over ten yards (Dowding, 1929). At this expulsion the viscid cells are torn across at the distal ends, so that the cell sap escapes. Thus the mucilage is provided by means of which the " seed " adheres to a host branch or other object in its path.

Expulsion of the " seed " takes place in late autumn. Germina-

tion may follow immediately or, more usually, is delayed until the following spring. The radicle grows, often for a considerable distance, along the surface of the substrate until an obstruction is met (Gill, 1935). At the obstruction an irregular mass of undifferentiated cells is formed, the " foot ", the nutrients for which are evidently provided by the older portion, as it soon withers and dies off. In the meantime the endosperm has been exhausted by the growing embryo, and some vascularization has begun, first in the radicle, later in the " foot ". The " foot " eventually sends down a haustorium-like projection, by means of which a new infection is established. The radicle by this time has completely deteriorated. Any aerial shoots formed in later years are produced adventitiously by the endophytic system and have no direct relation to the embryo.

Ecology of " Seed " Dispersal and Germination

Very little is known about the conditions prompting discharge of the " seed ". Many authors allude to certain moisture conditions necessary but fail to provide details. The distribution of one species, *A. pusillum,* was attributed to the high atmospheric humidity associated with coastal regions (von Schrenk, 1900). Further work on this phase of the life cycle is certainly needed before an explanation of the distribution of the parasite can be attempted.

Two other agencies which may aid the distribution of " seeds " are wind and animals. Wind is apparently of some importance or at least is most noticeable in those areas where winds are persistently from the same direction. Here the spread of *A. campylopodum* is clearly most rapid in the direction of the prevailing winds (Weir, 1916*a*; Roth, 1953). The possible role of animals in dissemination has been given somewhat more, though still superficial, attention. Suggestions of a speculative nature are to be found in von Schrenk (1900), Turrill (1920) and Buckland and Marples (1952), where some disjunct distributions of dwarf mistletoes are attributed to transportation of " seeds " by animals. Actual observations of English sparrows and grouse feeding on dwarf mistletoe berries were made by Weir (1916 *a, b*) and of finches and other birds by Gorrie (1929). Birds and rodents frequently build their nests in witches' brooms and so come into contact with the mistletoe plants. All authors, however, agree that the role of wind

and animals in the dissemination of " seeds " is of relatively minor significance.

As mentioned above, germination may begin in the fall or early spring. In the first case, growth of the radicle is often arrested during the cold season and resumed when proper conditions return. Weir (1918b) found that a higher percentage of germination was obtained when the " seeds " had undergone freezing temperatures, which fact may explain why most " seeds " in nature do not germinate until spring.

Heinricher made some observations on the germination of " seeds " of *A. oxycedri*. He noted that " seeds " on glass or inorganic material failed to germinate, while those on boards and filter paper did. From this evidence he concluded (1915a) that a stimulus went out from organic material (perhaps from cellulose) to effect germination. This view was also held by Palhinha (1942) who states that one of the conditions for germination is " almost certainly " some undetermined chemical stimulus. In a later paper, however, Heinricher (1917) corrected his earlier deductions, after finding that " seeds " germinate on both organic and inorganic substrates, as long as a sufficient supply of liquid water was present. In nature this requirement is possibly met by absorption of large quantities of water by the very hygroscopic mucilaginous layer. Several field observations by other workers (Peirce, 1905) confirm Heinricher's most recent views, viz., that dwarf mistletoe berries may germinate on any object provided moisture conditions are suitable.

An interesting feature of the germinating " seed " is the apparent presence of phototropism and geotropism. As early as 1888 Johnson recognized a distinct curvature of the radicle towards the host branch and assumed negative phototropism to be responsible for this movement. Heinricher (1917) confirmed this for another species and added that negative geotropism may also become evident. Extension of these studies is certainly warranted, where the later work of Tubeuf (1923) on the germination of *Viscum album* will be very suggestive.

It has been held by many workers that dwarf mistletoes can not become established on unwounded host tissues older than three years. Weir (1918b) believed this apparent resistance of older tissues to infection to be due to cork formation and the absence of

chlorophyll in the bark. By exposing older tissues which still contained some chlorophyll, he was able to effect establishment on branches up to seven years old. A recent worker, however, has shown that these assumptions can not be made in at least the parasitism of *A. americanum* on *Pinus contorta* (Hawksworth, 1954). This mistletoe was demonstrated to be able to become established through the bark of stems at least 58 years old. Furthermore, dissection of trunk infections indicated that establishment on tissues older than five years was of very frequent occurrence. These facts are of great silvicultural importance, and similar information of other hosts and dwarf mistletoes would contribute much essential knowledge to future control programs.

Physiology

Although no major physiological work has been conducted on dwarf mistletoes, several authors have submitted their ideas on some aspects of this field of study. *Arceuthobium* has been called totally parasitic (Cannon, 1901); it has been claimed that the genus is semi-parasitic, absorbing only water and nutrient salts (Heil, 1923); recent workers, however, regard it as inconceivable that the parasites manufacture all the food which they require (Gill, 1935).

Closely tied up with the question of dependency on the host is the presence of chlorophyll in dwarf mistletoes. Chlorophyll has been reported in several species, e.g., *A. oxycedri* (Heinricher, 1923) and *A. campylopodum* (Peirce, 1905), but not all species seem to be the same in this respect. For example, Heinricher found chloroplast-like bodies throughout the endophytic system of *A. oxycedri*, but Thoday and Johnson (1930) were unable to do so in *A. pusillum*. Many misstatements on the absence of chlorophyll are due to the fact that often brownish pigments in the epidermal cells mask the green tissues underneath. The presence of chlorophyll in the endophytic system seems somewhat problematic, since the light intensity there must be extremely low.

In a previous section it was mentioned that the anatomical evidence, though scarce, points to an absence of ordinary phloem tissue and its typical features. Although sieve plates have not been found to connect sieve tubes of the host and the living cells of the parasite, we are not justified in stating that no elaborated

food is absorbed from the host. Movement of nutrients through the thin separating walls in some places is inevitable because of different concentrations of dissolved food substances.

A feature which is encountered especially where broom formation takes place is the excessive storage of starch in host tissues at the point of infection and even in the endophytic mistletoe cells (Weir, 1918b). It is considered a direct result of the excessive flow of nutrients to the parasite. In time, however, a conspicuous starch deficiency develops at the infected parts (Heinricher, 1923), which may be attributable to interference in normal conduction or excessive local development of host branches into a witches' broom.

Most of the *Arceuthobium* species typically occur in dry locations, although some exceptions exist. Nevertheless it is obvious that the extreme morphological reduction is of great value in the many cases where dwarf mistletoes grow under very xeric conditions. Reduction in leaf surface, thickening of the outer walls of the epidermis, and screening of excessive radiation by other pigments are all very evident protective adaptations to conditions which, at least during certain seasons, approach desert conditions.

Meanwhile it must be kept in mind that the primary physiological requirement of a dwarf mistletoe plant is a suitable host. Exactly what determines the suitability of a particular host for a certain species of *Arceuthobium* is not yet known. Marked host affinities and antipathies unquestionably exist, but the extent of these has not been fully explored. Further inoculation experiments are therefore highly desirable.

HOST RELATIONSHIPS
Morphological Effects on Host

Among the economically and silviculturally important features of the dwarf mistletoes are the various aberrations of growth called forth in the host tree. These abnormalities may be divided into three main categories; intergrades, however, are common.

SWELLINGS AND CANKERS

A fusiform swelling on the young branch is frequently the first external evidence of the presence of a dwarf mistletoe. In most host species, infected branches become swollen to some extent. These swellings are due to both an abnormal increase in the pro-

duction of host xylem and phloem and to the mass of parasitic tissue (Heil, 1923). This initial hypertrophy may be followed by the development of witches' brooms, the component branches of which are likely to be conically swollen, i.e., broadest at their base with a marker taper. Infections by *A. campylopodum* characteristically result in such conically swollen branches. When infections involve the trunk of the tree, hypertrophies may develop without brooming. Such infections have serious economic importance and are also of great biological significance, as they undoubtedly shorten the life of the host (Gill, 1935).

Older swellings may eventually show areas of local necrosis. On the bole and large branches, these are often evident by the copious flow of resin from the necrotic area (Korstian and Long, 1922). A cross section of such a " resin canker " usually shows large areas of sapwood infiltrated with resin. This infiltration continues until the fibrovascular system is clogged with resin, killing the limb.

WITCHES' BROOMS

Heinricher (1918) was the first to point out that the ability to induce witches' brooms on host trees places the dwarf mistletoes in a unique position among flowering plants. Many other Loranthaceae grow into broom-like formations. The only other known plants that call forth this unusual growth from the host, however, are some parasitic fungi, for example, *Peridermium coloradense* (Dietel) Arth. and Kern on spruce.

That infection by dwarf mistletoe must inevitably lead to the formation of a witches' broom does not appear to be correct in all cases. The European species, *A. oxycedri,* is only occasionally associated with witches' brooms. The same is true of *A. minutissimum,* where, if brooms develop, they do so especially on dry sites (Gorrie, 1929). The situation in the North American species has not yet been fully analyzed.

Witches' brooms are typically dense masses of twiggy growth, varying greatly in size, even to the extent of involving whole trees (Gill, 1935). Brooms on *Tsuga* are horizontally flattened, those on *Larix* radiate out from a common area of origin, while those on the pines, spruces and Douglas-fir become more or less spherical. With certain reservations, Heinricher's (1918) observations on juniper have general application in North America. First, he

noted a local concentration of secondary branches. Secondly, the infected branches become negatively geotropic, emphasizing the broom-like appearance. A third feature may be added from North American examples, the elongation of individual branches of a witches' broom. That negative geotropism is not always found in brooms is shown by those caused by *A. douglasii* and others, where the branches often droop. Marked negative geotropism was, however, apparent in some North American cases, at least in the initial stages of broom formation (von Schrenk, 1900; Dowding, 1929). The morphological characteristics of a witches' broom, therefore, are partially determined by the nature of the branching in the host.

Occasionally witches' brooms may be several hundreds of pounds in weight (Buckland and Marples, 1952). It is not surprising to find, therefore, that the supporting branch is sometimes thicker than the main stem at their junction. One effect of this continuous weight is a marked eccentricity in annual growth of the supporting limb, more wood being formed in the lower half of the branch (Korstian and Long, 1922). It is also not surprising that brooms of great proportions have a very serious effect on the remaining uninfected part of the tree. In most North American mistletoe hosts, especially in Douglas-fir, " spike top " and similar features are a common sight in areas of infection. In these cases the drain of nutrients imposed by the broom gradually retards the growth of the healthy part to such an extent that the entire tree may be leafless with the exception of the witches' broom.

The best attempt at explaining the causal mechanism of broom formation is in one of Heinricher's publications on *A. oxycedri* (1918). He believed the formation to be related to the distribution of the parasite on the host. Experimentally it was found that *Juniperus*, when infected in only one place, developed a broom, while this did not take place where a large number of infections was present on one plant. The explanation offered for this difference was as follows. A localized infection may cause a flow of nutrients to the seat of infection, where storage of nutrients takes place to such an extent that the formation of buds and their development into branches are induced. When, however, many mistletoe plants are present on a juniper, these compete with one another. Therefore no food storage takes place, as the mistletoe uses all nutrients brought on, no surplus storage being present, no extra

branches or a witches' broom is formed. At once an objection to this theory seems present in the many North American examples where several to many witches' brooms are on a single tree. With some modifications, however, this theory may still hold for at least some of the other species.

OTHER EFFECTS

Aside from the above effects, mature mistletoe infections are usually accompanied by a variety of less tangible features. These have not been quantitatively studied but have much in common with the symptoms of other serious diseases. Some of these features may be mentioned separately.

The leaves of the infected branches, especially of brooms, are commonly distinctly shorter and often lighter in color than those of healthy branches. In *A. americanum* infections, leaves adhered to host branches several years longer than those on healthy ones (Dowding, 1929). In the case of *A. pusillum* the host branches were distinctly but uniformly thicker than normal ones (Thoday and Johnson, 1930).

A decrease of the radial increment of infected trees was determined with certainty in *Pinus ponderosa* (Korstian and Long, 1922), although this is probably a characteristic of most infections. However, an accelerated growth was noted in lightly infected trees, which may be due to a possible stimulating effect, as with minute quantities of many toxic substances.

Silviculturally it is significant that seed production is also influenced by mistletoe infection (Korstian and Long, 1922). With severity of infection there is a marked decrease in the percentage of germination, yield of cones and seed per tree, and consequently in the reproductive value per tree. On the other hand, lightly infected trees may experience a slight stimulating effect. The few cones occasionally on infected trees are often aborted or infested with insects. For these reasons, infected trees left for the purposes of seed production after logging are of very limited value.

Fungus and Insect Attack in Relation to Dwarf Mistletoe

The effect of most serious tree diseases is that the general vigor of the tree is eventually decreased to such a low level that the tree becomes more susceptible to other diseases as well. Mistletoe in-

fections are no exception to this rule, and in several places in the literature the association of mistletoe attack with that of some fungi and insects is recognized.

This increased susceptibility may result from a general decline in vigor or from local wounds in the infected tree. For example, the necrotic areas in mistletoe infections can easily serve as seats of infection, not only for bark- and wood-inhabiting fungi but also for certain insects. Weir (1916a) found larvae of the flat-headed fir borer (*Melanophila drummondi* Kirby) in many mistletoe burls. Korstian and Long (1922) found on trees, dead or dying from mistletoe infections, species of secondary bark beetles and borers, such as *Ips, Pityophthorus, Chrysobothris* and *Melanophila.* Also, the few cones occasionally borne on heavily infected trees are frequently infected with a cone insect (*Conophthorus ponderosae*). Significant is the statement of Buckland and Marples (1952) to the effect that healthy western hemlock withstood the effects of successive defoliations by the hemlock looper much better than those with dwarf mistletoe infections. Of a more speculative nature is the report of Korstian (1925) regarding a coincidence of the ranges of certain species of bark beetle and of dwarf mistletoe, and those of their hosts, two types of yellow pine. The significance of this indication, however, can not be fully evaluated until the taxonomic relationships of the dwarf mistletoes concerned are better known.

Secondary attack by fungi may become manifest in various ways. Necrotic areas on mistletoe infections provide an avenue of entrance for fungi, some of which may become established and girdle the branch. This frequently happens on mistletoe-infected branches of *Abies magnifica* in the Sierra Nevada, where *Cytospora* spp. are responsible for girdling (Gill, 1935). When witches' brooms are broken off and when mainstem infections develop into cankers at maturity of the tree, large open wounds are left on the trunk, facilitating the establishment of many of the most serious heart-rotting fungi, such as *Trametes pini* (Brot.) Fr. and *Echinodontium tinctorium* E. and E. (Hedgcock, 1915), eventually making the tree liable to windfall. In western hemlock, Englerth (1942) found that more than 30 per cent of decay in stands in western Oregon and Washington was traceable to mistletoe malformations, while Foster et al. (1954) made similar observations for the upper Columbia region of British Columbia.

Methods of Controlling Parasitism

Workers outside North America have not been concerned with the problem of how to control the destructive dwarf mistletoes. With the possible exception of *A. minutissimum,* which reduces the cover value of *Pinus excelsa* in the Himalayas, the species outside this continent are nowhere of economic importance, and no control is necessary. The importance of North American species has already been touched upon; but few, if any, of the following methods of control have emerged from the hypothetical or experimental stage.

CHEMICAL

The development of a great variety of selective herbicides within recent years has brought up the question whether one can be found to kill dwarf mistletoe without injury to the host. Considering the remoteness of relationship between hosts and parasites, it seems reasonable to expect that one of these selective chemicals might be effective. An initial study of this kind is in progress in Alberta (Bourchier, 1954). A systematic search, however, has not as yet been made. Of considerable interest are the results obtained by Greenham, et al. (1952), who found that trunk injections with 2,4-D showed some promise as control of *Loranthus* spp. on a *Eucalyptus* species in Australia. A full-scale investigation into the possibilities of chemical control of dwarf mistletoe is certainly warranted.

BIOLOGICAL

Biological agents of control may be divided into three groups: hyperparasitism by fungi, feeding by insects, feeding by birds and mammals.

FUNGI. Three fungi have been found parasitic on various species of *Arceuthobium.* None of these parasitic fungi is known outside North America.

The first parasitic fungus described on dwarf mistletoe is probably the most wide spread, certainly the most specific, of the three. *Wallrothiella arceuthobii* (Pk.) Sacc. (Sphaeriales, Ascomycetae) was first found by Peck (1875) on *A. pusillum* in the eastern United States, but subsequently in the West on the following hosts: *A. americanum, A. douglasii, A. campylopodum* f. *abietinum*

and f. *microcarpum* (Gill, 1935). The known range of this fungus in the West is from northern Alberta to Arizona, although quite local in occurrence.

The fungus is unusually specific in its requirements and has not yet been cultured. It attacks pistillate flowers only, allowing all except the inner tissues to develop. At maturity a black stroma and perithecia with club-shaped asci containing dark ascospores develop at the stigmatic region. *Wallrothiella* therefore interferes with reproduction by destroying the " seed ". Gill (1935) and Dowding (1931*b*) believe it of no practical consequence as an artificial biological control, particularly since it seems restricted to damp localities. A recent observer (Thomas, 1953), however, has found it commonly in dry localities and believes it to be of more consequence. The parasite was noted by the writer during the summer of 1953 in some very dry localities at Kimberley and Yellowhead Pass, B. C.

The second parasitic fungus on *Arceuthobium* has been known only since 1932. *Septogloeum gillii* Ellis (Fungi Imperfecti) was described by Ellis (1946) who found it to occur on stems (rarely on fruits) of several species. The fungus forms small yellowish-white lesions, often coalescing and erupting irregularly, liberating large masses of hyaline spores. Lesions are often concentrated near the nodes and are most common in summer and fall. Shoots of all ages may be attacked, but there appears to be a preference for pistillate plants. *Septogloeum gillii* has been found naturally on the following dwarf mistletoes: *A. americanum, A. douglasii, A. campylopodum* formae *abietinum, blumeri, cyanocarpum, divaricatum, microcarpum, tsugensis* and *campylopodum*. *A. vaginatum* f. *cryptopodum* was infected only after inoculation of wounds. Because of its virulent nature, this fungus is believed to have possibilities as a biological control.

The third fungus is known from one locality only, Point Lobos Reserve, California, where it was found on stems and leaves of *A. campylopodum*. It was named and described by Linder (1938) who called it *Metasphaeria wheeleri* Linder (Sphaeriales, Ascomycetae). It girdles stems, killing that portion of the stem beyond the infected area. The stems become yellowish and stand out in marked contrast to healthy brownish-green plants. As a biological control it probably has little value.

INSECTS. Several insects are known to feed upon species of dwarf mistletoe. Most of these are considered of little value in mistletoe control. Weir (1915) reported seeing grasshoppers feeding near Spokane, U.S.A., on yellow pine mistletoe (presumably *A. campylopodum* f. *campylopodum*). Heinricher (1915c) found shoots of *A. oxycedri* attacked by thrips. Spittle insects (Cercopidae) were found on *A. vaginatum* f. *cryptopodum* (Korstian and Long, 1922) and *A. campylopodum* f. *campylopodum* (Gill, 1935). Two Lepidoptera, *Mitoura spinetorum* Hew. (Comstock et al., 1938) and *Neoborella tumida* Knight (Knight, 1927), have been observed on *A. campylopodum* and *A. vaginatum* f. *cryptopodum*.

Of these insects spittle bugs are probably the most destructive to dwarf mistletoe plants. They mine out stems, causing death of the entire shoots. In some cases heavy mortality was noted (Gill, 1935). Older shoots were attacked primarily, and a partial check on reproduction may thus be imposed.

That more mistletoe-feeding insects exist seems very probable. The writer found larvae of an insect in stems of *A. campylopodum* f. *tsugensis* in the Botanical Gardens at the University of British Columbia, Vancouver, Canada. Stems were mined out completely, thereby killing the remainder of the shoot.

BIRDS AND MAMMALS. The interrelationships between dwarf mistletoes and vertebrate animals are very inadequately known; this is shown by the fact that only four brief references to vertebrates were located in the dwarf mistletoe literature. Weir (1916a) listed mistletoe berries and plants in the stomach of grouse, and observed English sparrows feeding on berries, which evidence is unequivocal and has its implications in the distribution of mistletoe " seeds ". Some rodents are known to prefer the swellings on mistletoe infections, and infected branches often show the signs of feeding by squirrels and porcupines (Korstian and Long, 1922; Taylor, 1935). Their preference for this spongy cortical mass may be attributable to the abundance of starch in such infections (Dufrenoy, 1936).

SILVICULTURAL

Attempts at silvicultural control have been directed mostly at the inhibition or restriction of normal " seed " distribution. Cer-

tain field observations provide a basis for possible control. The findings of Buckland and Marples (1952) may be mentioned first. Working with the hemlock mistletoe (*A. campylopodum* f. *tsugensis*) on western hemlock, three methods of logging were applied, and the resulting effect on the occurrence of the parasite observed. Where extensive clear-cutting took place, the subsequent reproduction showed mistletoe in some widely scattered locations only. Where only occasional trees or scattered blocks had been left, the mistletoe had rarely spread far into the reproduction. These trees did, however, serve as well-established centers of infection. Finally, where selective cutting was practiced, mistletoe was present throughout the new stand.

It is a well-recognized fact that the greatest spread of dwarf mistletoe is from overstory to understory (Gill and Andrews, 1942; Anderson and Kaufert, 1953; Roth, 1953). Uneven-aged stands are therefore more severely attacked than comparable even-aged ones. Also, mistletoe grows more rapidly after a part of the stand has been logged off, apparently because of improved light conditions (Korstian and Long, 1922). It is evident, therefore, that selective cutting ("high-grading") of a mistletoe-infected stand can lead to a very high degree of infection in the reproduction.

Theoretically mistletoe should be more amenable to control measures than many fungi. Mistletoe infections are confined to aerial parts of the tree, the "seeds" can not be carried along with the wind for any distance, and the parasite is killed with the death of the host, all of which are advantages, silviculturally, over most fungi. Complications arising from some logging practices have already been alluded to.

Also, control measures will have to be modified to suit the peculiarities of each species of mistletoe, some of which occur under quite different ecological conditions.

Many of the recommendations advanced for the management of mistletoe-infected forest stands can be applied to most species of the parasite. Silvicultural control methods must take into consideration the age of the stand concerned. For this purpose, Buckland and Marples (1952) offered the following suggestions for infected mature and overmature stands:

a) In clear-cutting, all residual trees and advanced reproduc-

tion should be destroyed. The clear-cut areas should be as large as can be allowed silviculturally.

b) When the block-system of cutting is used, mistletoe-infected blocks should be removed first.

c) If seed trees are to be left for reproductive purposes, they should be selected on their good form and apparent freedom from mistletoe.

For infected immature stands the following recommendations were given:

a) In any form of partial or selective cutting, all trees with mistletoe should be removed at the first cut, even to the extent of reducing the first cut to a non-profit operation.

b) Similarly, in any form of thinning, infected trees are to be removed first. An inspection, and removal of any infected trees previously overlooked, should be made no later than five years after the first treatment. This procedure was found to be sufficient to keep the parasite in check for all practical purposes (Anonymous, 1947).

When the infection concerns a relatively small part of the forest, it is feasible to stop the spread of the parasite by the establishment of a 60-foot mistletoe-free zone (Anonymous, 1949). In some of these cases, small timber sales or even free-use permits may be justified and effective (Weir, 1916*c*).

Working with *A. pusillum* on spruce, Anderson and Kaufert (1953) recognized a definite series of events in the development of an infection in an even-aged stand. The infection commonly starts in a small group of trees and slowly spreads outward, leaving the center of the infection in a state of destruction. The second generation in the vacated area is uneven-aged and heavily infected. The basis of the recommendations offered is the stage of development of the infection under consideration. In the initial stage, all broomed trees should be cut, as well as those within a zone of forty feet. In the second stage, when an opening, surrounded by broomed trees, is made in the canopy, the entire infected area plus a one-chain wide strip extending outward from the visibly broomed trees should be clear-cut. In this case, all spruce within this strip should be removed. In the later stage, a large area of ragged, uneven-aged and heavily infected trees is surrounded by a narrow zone of young reproduction and a belt of

broomed trees belonging to the original stand. To halt the advance of the mistletoe, the infected part of the surrounding stand plus a one-chain wide strip should be clear-cut immediately. Within this strip, all broomed merchantable trees should be cut, all non-merchantable trees either cut or pruned. This pruning treatment should include periodic repetition as described below.

Pruning methods are usually of little practical value in large-scale forest management but may be effective in small localities and in those where indivdual trees have high ornamental value, as on public camping grounds. Perry (1922) found a single pruning to be insufficient, since almost every tree developed mistletoe infections after pruning. The difficulty here lies in the fact that several years may be required for the germinating mistletoe plant to produce its first shoots. During this time the infection is practically invisible. If a pruning treatment is applied, therefore, it should be followed by a second treatment after the first mistletoe shoots have appeared of the infection thus hidden at the time of the first pruning, but before their production of fruits. It is unfortunate, for this reason, that data on the time elapsing between germination and the first flowering season for most species are not available. Also, the direction and rate of growth of the endophytic system are not accurately known (Gill, 1935). These gaps in our knowledge render any silvicultural treatment of dwarf mistletoes experimental. A recommendation to be kept in mind is that any such treatment, whether by logging or by pruning, should not be applied during the fruiting season (autumn), since the dispersal of " seeds " could be greatly assisted at this time.

Economic justification for any type of mistletoe control is naturally dependent on the value of the stand attacked. Mistletoe control procedures are at present rarely incorporated in silvicultural practices. Some trees attacked, such as western larch and white spruce, are not of great value as timber trees at localities of infection. It must be remembered, however, that the value of these trees quite possibly may go up to such an extent that control of their parasites will become necessary. In other trees, moreover, notably in western hemlock and Ponderosa pine, the damage due to mistletoe is of considerable magnitude and is liable to increase in succeeding generations unless more drastic measures are introduced (Gill, 1935).

One of the least known facets of the study of *Arceuthobium* is that concerned with the background of its distribution. Discrepancies between the ranges of most species and those of their hosts exist but are as yet unexplained. The Douglas-fir mistletoe (*A. douglasii*) is common on its host in many places throughout the latter's range east of the Cascades. Yet it has not been found on the Pacific Coast Douglas-fir. The factors limiting the distribution of this parasite are in urgent need of study for very convincing reasons; the economic importance of Douglas-fir on the Pacific Coast is indisputable, and the introduction of mistletoe could possibly be disastrous.

Among factors controlling the spread of dwarf mistletoe might be mentioned the distance between clumps of trees or individual trees (von Schrenk, 1900); high winds, which in certain areas may serve as natural pruning agents, breaking off heavy brooms (Weir, 1916a); and finally, the effect of forest fires (Dowding, 1929; Roth, 1953). Dowding, working on *A. americanum* in Alberta, states categorically that fire is of prime importance in limiting the distribution of this parasite. She argues that the spread of mistletoe in an even-aged stand is so slow that the stand is usually destroyed by a forest fire before the infection becomes serious. In the writer's view, however, the controlling influence of fires could be of significance only in a limited sense. These forest fires are the chief factor through which the extensive lodgepole pine forests on the east slopes of the Rocky Mountains remain extant. If the areas would be completely protected from fires, the lodgepole pine would, in time, probably be succeeded by a spruce–alpine fir stand, in which *A. americanum* would not survive. In a much broader sense than Dowding's, therefore, forest fires maintain the range of *A. americanum*. Furthermore, a forest fire usually leaves certain remnants of the forest untouched, which, if originally infected, soon becomes virulent centers of dissemination because of improved light conditions.

RECIPROCAL LIST OF HOSTS AND PARASITES

In the following list, the nature of the reference within brackets is indicated by exponents: [1] is given to those cases where infection was brought about artificially, no natural records being availa-

ble;[2] is given to those records which are believed to be rare host-parasite relations. If a host-parasite combination is commonly found, no further exponent is used; similarly, if a combination is rare in nature, artificial infections are not mentioned. Authorities are stated for parasites in the first, for hosts in the second section, only. In selecting references, those most complete, in the writer's opinion, were given preference.

By Parasite

[1]: artificially only; [2]: rarely

A. americanum Nutt. ex. Engelm.

Picea glauca[2]	(Bourchier and Kuijt, 1953)
Pinus albicaulis[2]	(Gill, 1935)
P. attenuata[2]	(Gill, 1935)
P. banksiana	(Gill, 1935)
P. contorta	(Gill, 1935)
P. edulis[2]	(Gill, 1935)
P. flexilis[2]	(Gill, 1935)
P. jeffreyi[2]	(Gill, 1935)
P. montana[1]	(Weir, 1918*b*)
P. ponderosa[2]	(Gill, 1935)

A. campylopodum Engelm.

Pinus muricata	(Howell, 1949)
P. occidentalis ?	(Urban, 1912)

A. campylopodum Engelm. f. *abictinum* (Engelm.) Gill

Abies amabilis[2]	(Gill, 1935)
A. arizonica[2]	(Gill, 1935)
A. concolor	(Gill, 1935)
A. grandis[2]	(Gill, 1935)
A. lasiocarpa[2]	(Gill, 1935)
A. magnifica	(Gill, 1935)
A. procera	(Gill, 1935)
A. shastensis	(Hedgcock, 1915)

f. *blumeri* (A. Nelson) Gill

Pinus lambertiana	(Gill, 1935)
P. monticola[2]	(Gill, 1935)
P. reflexa	(Gill, 1935)

f. *campylopodum* (Engelm.) Gill

Abies concolor [1]	(Weir, 1918*a*)
A. grandis [1]	(Weir, 1918*a*)
Larix europaea [1]	(Weir, 1918*a*)
L. occidentalis [1]	(Weir, 1918*a*)
Picea excelsa [1]	(Weir, 1918*a*)
Pinus attenuata	(Gill, 1935)
P. banksiana [1]	(Hedgcock and Hunt, 1917)
P. bungeana [1]	(Hedgcock and Hunt, 1917)
P. caribea [1]	(Hedgcock and Hunt, 1917)
P. contorta	(Gill, 1935)
P. coulteri	(Gill, 1935)
P. jeffreyi	(Gill, 1935)
P. montana [1]	(Weir, 1918*a*)
P. pinea [1]	(Hedgcock and Hunt, 1917)
P. ponderosa	(Gill, 1935)
P. radiata	(Gill, 1935)
P. resinosa [1]	(Weir, 1918*a*)
P. sabiniana	(Gill, 1935)
P. sylvestris [1]	(Weir, 1918*a*)
P. virginiana [1]	(Hedgcock and Hunt, 1917)

f. *cyanocarpum* (A. Nelson) Gill

Pinus albicaulis [2]	(Gill, 1935)
P. aristata [2]	(Gill, 1935)
P. balfouriana [2]	(Gill, 1935)
P. flexilis	(Gill, 1935)

f. *divaricatum* (Engelm.) Gill

Pinus cembroides	(Gill, 1935)
P. edulis	(Gill, 1935)
P. monophylla	(Gill, 1935)
P. parryana	(Gill, 1935)

f. *laricis* (Piper) Gill

Abies grandis [1]	(Weir, 1918*a*)
A. lasiocarpa [2]	(Weir, 1918*c*)
Larix europaea [1]	(Weir, 1918*a*)

L. leptolepis [1]	(Weir, 1918*a*)
L. lyallii	(Gill, 1935)
L. occidentalis	(Gill, 1935)
Picea engelmanni [2]	(Weir, 1918*c*)
Pinus albicaulis [2]	(Weir, 1918*c*)
P. contorta [2]	(Weir, 1918*c*)
P. monticola [2]	(Kuijt, 1953)
P. ponderosa [2]	(Weir, 1918*a*)

f. *microcarpum* (Engelm.) Gill

Picea breweriana [2]	(Gill, 1935)
P. engelmanni [2]	(Gill, 1935)
P. pungens [2]	(Gill, 1935)

f. *tsugensis* (Rosend.) Gill

Abies lasiocarpa [1]	(Weir, 1918*a*)
Tsuga canadensis [1]	(Weir, 1918*a*)
T. heterophylla	(Gill, 1935)
T. mertensiana	(Gill, 1935)

A. chinense Lec.

Abies sp.	(Lecomte, 1915)
Keteleeria sp.	(Handel-Mazetti, 1929)
Pinus tabulaeformis	(Handel-Mazetti, 1929)

A. douglasii Engelm.

Abies concolor [2]	(Hawksworth, 1952)
A. grandis [2]	(Weir, 1918*c*)
A. lasiocarpa [1]	(Weir, 1918*a*)
Picea engelmanni [2]	(Weir, 1918*c*)
Pseudotsuga macrocarpa	(Jepson, 1923)
P. menziesii	(Gill, 1935)

A. minutissimum Hook. f.

Pinus excelsa	(Hooker, 1886)

A. oxycedri (DC.) Bieb.

Chamaecyparis sphaeroidea [1]	(Heinricher, 1930)
Cupressus sp.[1]	(Heinricher, 1920)
Juniperus brevifolia	(Turrill, 1920)
J. communis	(Turrill, 1920)
J. drupacea	(Turrill, 1920)
J. excelsa	(Komarov, 1936)

J. oxycedrus	(Turrill, 1920)
J. phoenicea	(Turrill, 1920)
J. procera	(Turrill, 1920)
J. rufescens	(Turrill, 1920)
J. sabina	(Turrill, 1920)
J. semiglobosa	(Komarov, 1936)
J. seravschanica	(Komarov, 1936)
J. turcomanica	(Komarov, 1936)

A. pusillum Peck

Larix laricina [2]	(Jones, 1900)
Picea glauca	(Gill, 1935)
P. mariana	(Gill, 1935)
P. rubens	(Gill, 1935)
Pinus banksiana [2]	(Pomerleau, 1941)
P. resinosa [2] *	. . . .
P. strobus [2]	(House, 1935)

A. vaginatum (Willd.) Presl

Abies religiosa	(Gill, 1935)
Pinus arizonica	(Gill, 1935)
P. chihuahuana	(Hedgcock, 1915)
P. hartwegii	(Roldan, 1924)
P. jeffreyi	(Rydberg, 1917)
P. latifolia	(Gill, 1935)
P. leiophylla	(Gill, 1935)
P. ponderosa	(Gill, 1935)
P. tenuifolia †	. . . .

By Host

Abies amabilis (Dougl.) Forbes

A. campylopodum f. *abietinum* [2]	(Gill, 1935)

Abies arizonica Merr.

A. campylopodum f. *abietinum* [2]	(Gill, 1935)

Abies concolor Lindl. & Gord.

A. campylopodum f. *abietinum*	(Gill, 1935)
f. *campylopodum* [1]	(Weir, 1918a)
f. *laricis* [1]	(Weir, 1918a)
A. douglasii [2]	(Weir, 1918c)

* Specimen in Herbarium, University of Toronto, Ontario. Courtesy Mr. W. G. Ziller.
† Specimen in Herbarium, University of California, Berkeley, California.

Abies lasiocarpa (Hook.) Nutt.
    A. campylopodum f. *abietinum* [2]   (Gill, 1935)
                f. *laricis* [2]   (Weir, 1918*c*)
                f. *tsugensis* [1]   (Weir, 1918*a*)
    A. douglasii [1]   (Weir, 1918*a*)
Abies magnifica Murr.
    A. campylopodum f. *abietinum*   (Gill, 1935)
Abies procera Rehder
    A. campylopodum f. *abietinum*   (Gill, 1935)
Abies religiosa Lindl.
    A. vaginatum   (Gill, 1935)
Abies shastensis Lemmon
    A. campylopodum f. *abietinum* [2]   (Hedgcock, 1915)
Abies sp.
    A. chinense   (Lecomte, 1915)
Chamaecyparis sphaeroidea Spach
    A. oxycedri [1]   (Heinricher, 1930)
Cupressus sp.
    A. oxycedri [1]   (Heinricher, 1920)
Juniperus brevifolia Ant.
    A. oxycedri   (Turrill, 1920)
Juniperus communis L.
    A. oxycedri   (Turrill, 1920)
Juniperus drupacea Labill.
    A. oxycedri   (Turrill, 1920)
Juniperus excelsa Bieb.
    A. oxycedri   (Komarov, 1936)
Juniperus oxycedrus L.
    A. oxycedri   (Turrill, 1920)
Juniperus phoenicea L.
    A. oxycedri   (Turrill, 1920)
Juniperus procera Hochst. ex Endl.
    A. oxycedri   (Turrill, 1920)
Juniperus rufescens Link
    A. oxycedri   (Turrill, 1920)
Juniperus sabina L.
    A. oxycedri   (Turrill, 1920)
Juniperus semiglobosa Regel
    A. oxycedri   (Komarov, 1936)

Juniperus seravschanica Komar.
    A. oxycedri   (Komarov, 1936)
Juniperus turcomanica Fedtsch.
    A. oxycedri   (Komarov, 1936)
Keteleeria sp.
    A. chinense   (Handel-Mazetti,
                                              1929)

Larix europaea DC.
    A. campylopodum f. *campylopodum* [1]   (Weir, 1918*a*)
                f. *laricis* [1]   (Weir, 1918*a*)
Larix laricina (Du Roi) Koch
    A. pusillum [2]   (Jones, 1900)
Larix leptolepis Hort. ex Endl.
    A. campylopodum f. *laricis* [1]   (Weir, 1918*a*)
Larix lyallii Parl.
    A. campylopodum f. *laricis*   (Gill, 1935)
Larix occidentalis Nutt.
    A. campylopodum f. *campylopodum* [1]   (Weir, 1918*a*)
                f. *laricis*   (Gill, 1935)
Picea breweriana Watson
    A. campylopodum f. *microcarpum* [2]   (Gill, 1935)
Picea engelmanni Parry
    A. campylopodum f. *microcarpum* [2]   (Gill, 1935)
                f. *laricis* [2]   (Weir, 1918*c*)
    A. douglasii [2]   (Weir, 1918*c*)
Picea excelsa Link
    A. campylopodum f. *campylopodum* [1]   (Weir, 1918*a*)
Picea glauca (Moench) Voss
    A. americanum [2]   (Bourchier and Kuijt,
                                              1953)
    A. pusillum   (Gill, 1935)
Picea mariana (Mill.) B. S. P.
    A. pusillum   (Gill, 1935)
Picea pungens Engelm.
    A. campylopodum f. *microcarpum* [2]   (Gill, 1935)
Picea rubens Sarg.
    A. pusillum   (Gill, 1935)
Pinus albicaulis Engelm.
    A. americanum [2]   (Gill, 1935)

A. campylopodum f. *cyanocarpum* [2]   (Gill, 1935)
          f. *laricis* [2]   (Weir, 1918*c*)
Pinus aristata Engelm.
  A. campylopodum f. *cyanocarpum* [2]   (Gill, 1935)
Pinus arizonica Engelm.
  A. vaginatum   (Gill, 1935)
Pinus attenuata Lemmon
  A. americanum [2]   (Gill, 1935)
  A. campylopodum f. *campylopodum*   (Gill, 1935)
Pinus balfouriana Jeffrey ex Murray
  A. campylopodum f. *cyanocarpum* [2]   (Gill, 1935)
Pinus banksiana Lamb.
  A. americanum   (Gill, 1935)
  A. campylopodum f. *campylopodum* [1]   (Hedgcock and Hunt, 1917)
  A. pusillum [2]   (Pomerleau, 1941)
Pinus bungeana Zucc.
  A. campylopodum f. *campylopodum* [1]   (Hedgcock and Hunt, 1917)

Pinus cembroides Gord.
  A. campylopodum f. *divaricatum*   (Gill, 1935)
Pinus chihuahuana Engelm.
  A. vaginatum   (Hedgcock, 1915)
Pinus contorta Dougl. ex Loud.
  A. americanum   (Gill, 1935)
  A. campylopodum f. *campylopodum*   (Gill, 1935)
          f. *laricis* [2]   (Weir, 1918*c*)
Pinus coulteri Don.
  A. campylopodum f. *campylopodum*   (Gill, 1935)
Pinus edulis Engelm.
  A. americanum [2]   (Gill, 1935)
  A. campylopodum f. *divaricatum*   (Gill, 1935)
Pinus excelsa Wall. ex Lamb.
  A. minutissimum   (Hooker, 1886)
Pinus flexilis James
  A. americanum [2]   (Gill, 1935)
  A. campylopodum f. *cyanocarpum*   (Gill, 1935)
Pinus hartwegii Lindl.
  A. vaginatum   (Roldan, 1924)

Pinus jeffreyi Murr.
   A. americanum [2]   (Gill, 1935)
   A. campylopodum f. *campylopodum*   (Gill, 1935)
   A. vaginatum   (Gill, 1935)
Pinus latifolia Sarg.
   A. vaginatum   (Gill, 1935)
Pinus lambertiana Dougl.
   A. campylopodum f. *blumeri*   (Gill, 1935)
Pinus leiophylla Schlecht. & Cham.
   A. vaginatum   (Gill, 1935)
Pinus monophylla Torr. & Frém.
   A. campylopodum f. *divaricatum*   (Gill, 1935)
Pinus montana Mill.
   A. americanum [1]   (Weir, 1918*b*)
   A. campylopodum f. *campylopodum* [1] (Weir, 1918*b*)
Pinus monticola Dougl. ex Lamb.
   A. campylopodum f. *blumeri* [2]   (Gill, 1935)
                f. *laricis* [2]   (Kuijt, 1953)
Pinus muricata Don.
   A. campylopodum   (Howell, 1949)
Pinus occidentalis Sw.
   A. campylopodum ?   (Urban, 1912)
Pinus parryana Engelm.
   A. campylopodum f. *divaricatum*   (Gill, 1935)
Pinus pinea L.
   A. campylopodum f. *campylopodum* [1] (Hedgcock and Hunt, 1917)

Pinus ponderosa Dougl. ex Laws.
   A. americanum [2]   (Gill, 1935)
   A. campylopodum f. *campylopodum*   (Gill, 1935)
                f. *laricis* [2]   (Weir, 1918*a*)
   A. vaginatum   (Gill, 1935)
Pinus radiata Don.
   A. campylopodum f. *campylopodum*   (Gill, 1935)
Pinus resinosa Ait.
   A. campylopodum f. *campylopodum* [1] (Weir, 1918*a*)
   A. pusillum [2]   (See footnote *, p. 606)
Pinus sabiniana Dougl.
   A. campylopodum f. *campylopodum*   (Gill, 1935)

Pinus reflexa (Engelm.) Engelm.
 A. campylopodum f. *blumeri* [2] (Gill, 1935)
Pinus strobus L.
 A. pusillum [2] (House, 1935)
Pinus sylvestris L.
 A. campylopodum f. *campylopodum* [1] (Weir, 1918*a*)
Pinus tabulaeformis Hort. ex Carr.
 A. chinense (Handel-Mazetti,
            1929)
Pinus tenuifolia Benth.
 A. vaginatum (See footnote †, p. 606)
Pinus virginiana Mill.
 A. campylopodum f. *campylopodum* [1] (Hedgcock and Hunt,
            1917)
Pseudotsuga macrocarpa (Torr.) Mayr.
 A. douglasii (Jepson, 1923)
Pseudotsuga menziesii (Mirb.) Franco
 A. douglasii (Gill, 1935)
Tsuga canadensis (L.) Carr.
 A. campylopodum f. *tsugensis* [1] (Weir, 1918*a*)
Tsuga heterophylla (Raf.) Sarg.
 A. campylopodum f. *tsugensis* (Gill, 1935)
Tsuga mertensiana (Bong.) Sarg.
 A. campylopodum f. *tsugensis* (Gill, 1935)

SELECTED ILLUSTRATIONS

1. *A. americanum.*
  Present paper, Plate I, Fig. 1. (Male plant)
       Plate II, Fig. 5. (Female plant)
2. *A. campylopodum* f. *abietinum.*
  Weir (1918*b*), Figs. 7, 8. (Male and female plants)
3. *A. campylopodum* f. *blumeri.*
  Gill (1935), Plate IX.
4. *A. campylopodum* f. *campylopodum.*
  Weir (1918*b*), Figs. 1, 2. (Male and female plants)
5. *A. campylopodum* f. *cyanocarpum.*
  Gill (1935), Plate X.
6. *A. campylopodum* f. *divaricatum.*
  Gill (1935), Plate VIII.

7. *A. campylopodum* f. *laricis.*

    Present paper, Plate I, Fig. 4; Plate II, Fig. 8. (Female
        plants)

        Plate II, Figs. 6, 7. (Male plants)

8. *A. campylopodum* f. *tsugensis.*

    Present paper, Plate I, Fig. 2. (Male plant)

    Rosendahl (1903), Plate XXVII. (Male and female
        plants)

9. *A. douglasii.*

    Gill (1935), Plate VI. (Female plants)

    Present paper, Plate I, Fig. 3. (Male plants)

10. *A. minutissimum.*

    Gorrie (1929), Plate 31. (Main stem infection)

11. *A. oxycedri.*

    Heinricher (1918), Tafel III, Fig. 5.

12. *A. pusillum.*

    Jack (1900), Plate 13.

13. *A. vaginatum.*

    Gill (1935), Plate XI.

14. The Endophytic System.

    Thoday and Johnson (1930), Text-figs. 2–9; Plate
        XXIII, Figs. 3, 4.

        Drawings of endophytic strands in longitudinal and
        cross-section; development of buds; dissection of
        endophytic system along a host branch.

               A. pusillum.

15. Stem and Leaves. (See individual species)

    Gill (1935), Plate IV, A, B.

        Differences in branching of *A. americanum* and *A.*
        campylopodum.

16. Male Flowers.

    Gill (1935), Figs. 1, 2.

        Staminate flower and shoot; diagram of open flower.

               A. americanum.

        Plate III, A.

        Shoot with staminate flowers, open and in bud.

               A. campylopodum.

    Dowding (1931*a*), Figs. 1–3.

        Variations in shape of sterile column in anther.

               A. americanum.

Pomerleau (1941), Fig. 3.
  Male shoot and flowers.
                        A. pusillum.
Heinricher (1915*b*), Tafel I, Figs. 4–6.
Erdtmann (1952), Fig. C, p. 250.
  Pollen grains.
                        A. oxycedri.

17. Female Flowers.
  Gill (1935), Plate III, B.
    Pistillate shoot, lateral and terminal flowers.
                        A. campylopodum.
  Heinricher (1915*b*), Plate I, Fig. 7.
    Receptive flowers, oil droplets.
                        A. oxycedri.
  Johnson (1888), Plate X, Figs. 1–7.
    Longitudinal sections; detailed enlargements, trans-
    verse sections at different levels.
                        A. oxycedri.
  Dowding (1931*a*), Figs. 4–11.
    Longitudinal section; variations in fusion of carpels;
    floral diagrams of terminal clusters.
                        A. americanum.

18. Fruit.
  Gill (1935), Fig. 7.
    Diagrammatic longitudinal section.
                        A. vaginatum.
  Present paper, Plate II, Fig. 8.
    Mature berries.
                        A. campylopodum f. *laricis.*
  Johnson (1888), Plate X, Figs. 8–12.
    Surface view; sections, cellular detail.
                        A. oxycedri.
  Peirce (1905), Plate III, Figs. 3–10.
    Longitudinal and other sections; cellular detail.
                        A. campylopodum.

19. Germination.
  Peirce (1905), Plate IV, Figs. 14–19.
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                        A. campylopodum.

Heinricher (1915*d*), Plates I, II, III.
>   Series of stages.   (in color)
>> *A. oxycedri.*

20. Swellings.
>   Buckland and Marples (1952), Fig. 6.
>> Large trunk swelling on *Tsuga heterophylla.*
>>> *A. campylopodum* f. *tsugensis.*
>   Weir (1916*b*), Fig. 19.
>> Burls on *Pinus ponderosa.*

21. Witches' Brooms.
>> *A. americanum.*
>   Present paper, Plate III, Fig. 9.   (on *Pinus ponderosa*)
>>> Fig. 10.   (on *Picea glauca*)
>>> Fig. 11.   (on *Pinus banksiana*)
>>> Fig. 12.   (on *Pinus contorta*)
>> *A. campylopodum* f. *laricis.*
>   Present paper, Plate IV, Fig. 13.   (on *Larix occidentalis*)
>> *A. campylopodum* f. *tsugensis.*
>   Buckland and Marples (1952), Fig. 8.   (on *Tsuga heterophylla*)
>> *A. douglasii.*
>   Present paper, Plate IV, Fig. 14.   (on *Pseudotsuga taxifolia*)
>> *A. minutissimum.*
>   Gorrie (1929), Plate 31.   (on *Pinus excelsa*)
>> *A. oxycedri.*
>   Heinricher (1918), Tafel I, Fig. 1; Tafel III, Fig. 5. (on *Juniperus communis*)
>> *A. pusillum.*
>   Yuncker (1930), Figs. 1, 2.   (on *Picea mariana*)
>   Jones (1900), Plate 14.   (on *Larix laricina*)
>> *A. vaginatum.*
>   Korstian and Long (1922), Plate III, Fig. 1.   (on *Pinus ponderosa*)

22. Hyperparasites.
>> *Wallrothiella arceuthobii.*
>   Dowding (1931*b*), Plate I, Figs. 4, 5; Text-figs. 1–21.
>>> Plate II, Figs. 1–3.
>>> On *A. americanum* on *Pinus banksiana.*   Infected fruit; longitudinal sections; spore

emergence, ascospores and asci; germination
of stroma; mycelium and sprout cells.

Present paper, Plate IV, Fig. 15.

On *A. americanum* on *Pinus contorta*.

Septogloeum gillii.

Ellis (1946), Text-fig. 2; Plates 4, 5, 6.

Conidia and conidiophores; lesions on shoots of
A. campylopodum; sections of fruiting layer
and infected stem; lesions on stems of *A.
vaginatum* and *A. douglasii*.

Metasphaeria wheeleri.

Linder (1938), Fig. 1.

Perithecium, paraphyses, asci and ascospores.

23. Distribution Maps.

Foster and Ziller (1952), p. 154.

Distribution of *A. campylopodum* f. *tsugensis* in
British Columbia.

Bourchier (1953), p. 126.

Distribution of *A. americanum* in Alberta.

Thomas (1953), pp. 98, 99.

Distribution of *A. pusillum* in Saskatchewan and
Manitoba.

Distribution of *Wallrothiella arceuthobii* in Sas-
katchewan.

ACKNOWLEDGEMENTS

The writer wishes to express his sincere appreciation to Dr.
T. M. C. Taylor, Department of Biology and Botany, University
of British Columbia, Vancouver, for his many valuable suggestions
and guidance throughout the review; to Dr. V. J. Nordin, Officer-
in-Charge, Forest Pathology Laboratory, Calgary, for his assist-
ance in the preparation of this report; and to various members of
his staff, in particular to Miss J. Hewitt, for the preparation of the
photographic plates. A word of thanks is also due to Dr. Adriance
S. Foster, University of California at Berkeley, for criticizing the
revised section on the endophytic system.

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PLATE I

Common Host-Parasite Associations

FIG. 1. *Arceuthobium americanum* (male) on *Pinus contorta*. Kananaskis,
        Alberta.   Ca. × 1.
FIG. 2. *A. campylopodum* f. *tsugensis* (male) on *Tsuga heterophylla*.
        Vancouver, B. C.   Ca. × ½.
FIG. 3. *A. douglasii* (male) on *Pseudotsuga taxifolia*. Kootenay Lake,
        B. C.   Ca. × 1.
FIG. 4. *A. campylopodum* f. *laricis* (female) on *Larix occidentalis*. St.
        Mary's Lake, B. C.   Ca. × 1.

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PLATE II

Unusual Host-Parasite Associations

FIG. 5. *Arceuthobium americanum* (female) on *Picea glauca*. Kananaskis, Alberta. Ca. × 2.

FIG. 6. *A. campylopodum* f. *laricis* (male) on *Pinus contorta*. Christina Lake, B. C. Ca. × 1.

FIG. 7. *A. campylopodum* f. *laricis* (male) on *Pinus monticola*. Slocan Lake, B. C. Ca. × ½.

FIG. 8. *A. campylopodum* f. *laricis* (female) on *Pinus monticola*. Slocan Lake, B. C. Ca. × 1.

PLATE III

Witches' Brooms

FIG. 9. *Arceuthobium americanum* on *Pinus ponderosa*. Kimberley, B. C
FIG. 10. *A. americanum* on *Picea glauca*. Kananaskis, Alberta.
FIG. 11. *A. americanum* on *Pinus banksiana*. Calling Lake, Alberta.
FIG. 12. *A. americanum* on *Pinus contorta*. Banff, Alberta.

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PLATE IV

Witches' Brooms (Continued)

Fig. 13   *Arceuthobium campylopodum* f *laricis* on *Larix occidentalis*
           St Mary's Lake, B C
Fig. 14   *A douglasii* on *Pseudotsuga taxifolia*   Kootenay Lake, B C

Hyperparasitism

Fig. 15   *Wallrothiella arceuthobii*, parasitic on berries of a female colony
           of *A americanum* on *Pinus contorta*   Kootenay National Park,
           B C   Ca × 1.